DISSERTATION

THE EFFECTS OF URBANIZATION ON FELID POPULATIONS, INTERACTIONS, AND PATHOGEN DYNAMICS

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ABSTRACT

THE EFFECTS OF URBANIZATION ON FELID

POPULATIONS, INTERACTIONS, AND PATHOGEN DYNAMICS

Urbanization is one of the most ecologically impactful forms of landscape conversion with far-reaching effects on landscape pattern and process, particularly related to animal populations. We evaluated how urbanization affected population density, interspecific interactions, and pathogen exposure in wild felid populations. Specifically, we studied bobcats and pumas across wildland, exurban development, and wildland-urban interface (WUI) habitat to test hypotheses evaluating how urbanization impacts wild felids. Low-density residential development appeared to have a greater impact on felid population density compared to habitat adjacent to a major urban area; point estimates of population density were lower for bobcats and pumas in exurban development compared to wildland habitat, whereas population density for both felids appeared more similar between WUI and wildland habitat. For competitive interactions, occupancy modeling indicated that bobcats did not avoid pumas across broad spatial and temporal scales; however, at finer scales bobcats temporally avoided pumas in wildland areas, but did not appear to avoid pumas in urbanized habitat. Using telemetry data, contact networks revealed that space-use extent was an important predictor of possible social interactions, but that felids associated with urbanization did not appear to exhibit increased potential for interspecific interactions. Lastly, we provided a conceptual framework for evaluating the effects of multiple ecological mechanisms on patterns of pathogen exposure in animal populations; we demonstrated how demographic, social, and environmental

characteristics affected the pathogen exposure in bobcat and puma populations across a gradient of urbanization.

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OVERVIEW

Urbanization is one of the most ecologically impactful forms of landscape conversion with far-reaching effects on landscape pattern and process, particularly related to the population characteristics of animals. Urbanization can alter animal movement and habitat quality, both of which can influence population abundance and persistence. We evaluated three important population characteristics (population density, site occupancy, and species detectability) of medium- and large-sized carnivores across a gradient of urbanization. Specifically, we studied bobcat and puma populations across wildland, exurban development, and wildland-urban interface (WUI) habitat to test hypotheses evaluating how urbanization impacts wild felid populations and their prey. Low-density residential development had a greater impact on felid populations compared to habitat adjacent to a major urban area; population density for both bobcats and pumas appeared to be lower in areas of exurban development compared to wildland areas, whereas population density appeared similar between WUI and wildland habitat. Occupancy of both felids was similar between wildland areas and habitat influenced by urbanization, indicating that this population metric was less sensitive than density. Bobcats and pumas were less likely to be detected in habitat as the amount of human disturbance associated with residential development increased at a site. At the scale of the sampling grid, detection probability for bobcats in urbanized habitat was greater compared to wildland areas, potentially

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due to restrictive movement corridors and funneling of animal movements in landscapes influenced by urbanization. Occupancy of important felid prey (cottontail rabbits and mule deer) was high and generally similar along the gradient of urbanization, suggesting availability of these key prey species was similar among sampling areas, although elk occupancy was lower in urbanized areas. Our study indicates that the conservation of medium- and large-sized carnivores associated with urbanization will likely be most successful if large areas of wildland habitat are maintained, even in close proximity to urban areas, and wildland habitat is not converted to low-density residential development.

INTRODUCTION

Urbanization, ranging from low- to high- density residential development, is a leading agent of broad-scale landscape change that can substantially alter ecological patterns, processes, and communities (Chace and Walsh 2006, Shochat et al. 2006, McKinney 2008) and is projected to be a primary cause of landscape fragmentation and biodiversity loss over the next century (Sala et al. 2000, Seto et al. 2012). By influencing habitat selection, space use, and fitness of animals, urbanization can impact wildlife populations in contrasting ways (McKinney 2002, Hansen et al. 2005, Crooks et al. 2010, Riley et al. 2010). Urbanization can increase population density by restricting animal movement, increasing available forage, or decreasing competition by reducing the population size of competitors (e.g., Crooks and Soulé 1999, Prange et al. 2003, Riley et al. 2006). In contrast, urbanization can decrease population density by reducing habitat quality and quantity, increasing human disturbance, or increasing the population density of competitors (e.g., Bolger et al. 1997, Germaine and Wakeling 2001, Merenlender et al. 2009). Thus, although urbanization homogenizes landscape pattern (McKinney 2006) and results in

population declines and reduced diversity for many native species, the juxtaposition and integration of human development with natural areas can also increase landscape heterogeneity and food resources (Murcia 1995, Irwin and Bockstael 2007) and produce greater biodiversity and abundance of some species (McKinney 2008).

Although all types of urban development can influence animal movement, habitat suitability, and ultimately population characteristics, different forms of urbanization affect these factors to varying degrees. For example, high-density development, characterized by urban (< 0.25 acres per residence) and suburban (0.25 – 1.68 acres per residence) areas (Theobald 2005), can create relatively impermeable anthropogenic barriers that restrict movement, inflate density, and alter habitat. The juxtaposition of residential development with wildland habitat (i.e., primarily natural habitat without human development) creates a wildland-urban interface (WUI), which is often characterized by a linear boundary that can significantly alter ecological processes (Radeloff et al. 2005). The "fence effect" (Krebs et al. 1969) and "island syndrome" (Adler and Levins 1994) hypotheses propose that populations that are bounded on all sides spatially (e.g., populations in a fenced enclosure, on an isolated island, or in an urban habitat fragment) exhibit higher densities compared to populations not bounded due to restricted dispersal. Further, populations bounded on only one side of their spatial extent have also been reported to exhibit altered population characteristics. The "home-range pile-up" hypothesis predicts that a linear anthropogenic barrier can influence space use and emigration patterns of populations leading to elevated population densities (Riley et al. 2006). Specifically, bobcats (*Lynx rufus*) in a highly urbanized environment were reported to reach abnormally high population densities adjacent to a major highway compared to populations away from this barrier (Riley et al. 2006).

Other forms and configurations of residential development might not create impermeable barriers to animal movement, but can still considerably influence landscape pattern and heterogeneity and thus habitat characteristics and prey resources. For instance, exurban (1.68 – 40 acres per residence) and rural (> 40 acres per residence) development is characterized by relatively low density urbanization that is often immersed within wildland landscapes (Theobald 2004, Brown et al. 2005, Theobald 2005) and can permeate over much broader spatial extents compared to linear boundaries created by wildland-urban interfaces. Such development often occurs adjacent to wildland areas and can increase landscape heterogeneity through edge effects (Murcia 1995). Thus, low-density urbanization may benefit some species by increasing habitat diversity and food resources and be permeable to animal movement for travelling and foraging (Gehrt et al. 2010). Nonetheless, anthropogenic disturbance within exurban and rural landscapes can also reduce habitat suitability and quality, animal fitness, and ultimately population density (Hansen et al. 2005, McKinney 2008).

Carnivores are particularly sensitive to altered landscape configuration and composition resulting from human activities due to their life-history characteristics, including low population densities, low birth rates, large home ranges, wide-ranging movements, and social structure (Noss et al. 1996, Gittleman et al. 2001, Cardillo et al. 2005). Mammalian carnivores, however, differ in their vulnerability to urban fragmentation (Crooks 2002). Large carnivores, such as pumas (i.e., cougar, mountain lion, panther; *Puma concolor*), are typically most sensitive to urban fragmentation and most likely to occur in large patches of habitat that are connected to other large natural areas (Crooks 2002, Beier et al. 2010). In comparison, medium-sized carnivores, such as bobcats, may be less sensitive to fragmentation and exhibit greater tolerance to urban development given suitable habitat and landscape connectivity (Crooks 2002, Riley et

al. 2010). Although obtaining reliable information about carnivore populations has proven challenging due to their life-history characteristics and secretive nature, recent methodological developments, such as motion-activated cameras (O'Connell et al. 2010), have better enabled researchers to study their populations.

Our goal was to evaluate how different landscape configurations across a gradient of urbanization influenced the population characteristics of two carnivores, the bobcat and puma, with varying sensitivities to human impacts. We evaluated how three key ecological parameters – population density, site occupancy, and species detectability (collectively referred to as population characteristics) – differed among landscapes influenced by varying levels of urbanization, ranging from wildland-urban interface to exurban to wildland habitat. Specifically, we estimated population characteristics for bobcats and pumas to evaluate (1) the home-range pile-up hypothesis in relation to a wildland-urban interface and (2) how felid populations responded to low density residential development. In addition to estimating population characteristics of felids, we also estimated occupancy of key prey species to evaluate potential differences in available food resources of carnivores along the urban gradient. If residential development restricts movement and inflates felid density, as predicted by the home-range pile-up hypothesis (Riley et al. 2006), or if it enhances landscape heterogeneity and carnivore prey populations, as might particularly be the case in low-density residential development, we would expect higher population characteristics of felids associated with these areas. Conversely, if felids avoid residential development due to human disturbance and reduced habitat suitability, we would expect lower population characteristics in such areas. By evaluating the impacts of different forms of urbanization on wild felid populations we provide novel and important

information about wildlife conservation in landscapes influenced by exurban and urban development.

STUDY AREA

We conducted our research across two study sites in Colorado, USA that exhibited varying degrees of urbanization and human influence. Within each study area, we evaluated felid populations that occurred on two grids that were characterized by similar habitat and landscape characteristics, but differed in the degree of urbanization. Extensive areas of habitat that supported felid populations surrounded both of our study areas.

In 2009 and 2010, we worked on the Western Slope (WS) of Colorado on the relatively rural Uncompahgre Plateau near the towns of Montrose and Ridgway (Figure 1). The area was characterized by mesas, canyons, and ravines, with elevations ranging from 1800 m to 2600 m and annual precipitation of 43 cm arriving primarily from winter snows and summer thunderstorms (NOAA National Climatic Data). Common vegetation included pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), gambel oak (*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). The WS exhibited extensive areas of undeveloped wildland habitat managed by the Bureau of Land Management (BLM), US Forest Service (USFS), and private landowners. Paved and unimproved roads occurred throughout the WS. The WS has a history of ranching and some private ranches were converted into exurban and rural housing developments. We divided the WS study site into two sampling grids. The southern grid 1 sampled exurban and rural residential development on Log Hill Mesa (population = 1,041; US Census Bureau 2010); residential parcel sizes were distributed, from most to least numerous, across 5 acre, 2 acre, 1

acre, ≥ 5 acre, and ≥ 40 acre properties. Within areas of exurban development, travel corridors of natural habitat and open space property, often with associated recreation trails, were present. The northern grid 2 sampled primarily undeveloped, wildland habitat, although some small areas of low density human residences and hunting camps occurred on or near the grid.

In 2010 to 2012, we worked on the more urbanized Front Range (FR) of Colorado (Figure 1). The area was characterized by gentle foothills and valleys, ravines and canyons, and mountainous terrain, with elevations ranging from 1600 m to 2500 m and annual precipitation of 53 cm, arriving primarily from winter snow and summer thunderstorms (NOAA National Climatic Data). Common vegetation included ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), juniper, aspen, and mountain mahogany (*Cercocarpus montanus*). An extensive network of open space properties with recreational trails were managed by Boulder City Open Space and Mountain Parks (OSMP) and Boulder County Parks and Open Space (BCPOS). The USFS and BLM also managed undeveloped land on the western portion of the FR study area. Paved and unimproved roads occurred throughout much of the FR, although several areas were only accessible by trail. Similar to the WS, we divided the FR study area into two sampling grids. The southern grid 1 occurred adjacent to the wildland-urban interface associated with the city of Boulder (population = 97,385, US Census Bureau 2010) and was characterized by OSMP and BCPOS open-space properties with some human residences on or near the grid. The northern grid 2 occurred across undeveloped BCPOS and USFS properties, although a small number of human residences occurred on private property inholdings. Short-grass prairie, agricultural fields, and associated riparian corridors occurred to the east of both sampling grids and surrounded the city of Boulder.

METHODS

Sampling Grids and Camera Surveys

Each study area (WS and FR) contained 40 motion-activated cameras divided between 2 camera grid arrays spaced approximately 6 km apart (Figure 1). Each grid was 80 km^2, consisting of 20 2 x 2 km grid cells (both grids in each study area sampled a total of 160 km^2). Our study design was consistent with a retrospective observational study (Williams et al. 2002) that contained experimental components of a treatment (exurban grid 1 on the WS and wildland-urban interface grid 1 on the FR) and control (wildland grids 2 on the WS and FR).

Within each grid cell, we placed one motion-activated camera at a site that we believed maximized the opportunity to photograph bobcats and pumas. Cameras were placed along game trails, people trails, and secondary dirt roads with felid sign (primarily scats, scrapes, and marking sites) or in areas that appeared to be likely travel routes. Our sampling was passive in that we did not use attractants (i.e., sight, sound, scent) to lure animals to the camera location. We used Cuddeback (Non Typical, Inc., Green Bay, WI, USA) Capture motion-activated cameras (with a 30 second delay) with a white-flash to obtain color photographs during the day and at night, except at one site along a high-use human recreation trail on the FR where we switched to using a Cuddeback Attack Infra-Red camera to reduce vandalism. Cameras operated on the WS from 21 August to 13 December 2009 and on the FR from 1 October 2010 to 31 December 2010.

We considered photographs of bobcats and pumas taken at a camera site to be independent if images were obtained >1 hour apart. If 2 adult felids were photographed <1 hour apart and could be differentiated based on natural or artificial (i.e., telemetry collars and eartags) markings, these photographs were also counted as independent animals. Kittens and dependent

offspring (individuals typically of small body size and often accompanied by their mother in photographs) were not considered independent animals and were excluded from analyses.

Animal Capture

Bobcats were captured in black metal-wire cage traps (40 x 55 x 100 cm) with attractants from mid-June through March 2009 – 2011. All cage traps were fit with very high frequency (VHF) trap transmitters (Telonics Inc., Mesa, AZ, USA) that indicated when trap doors closed. Captured bobcats were immobilized through hand-injection of a combination of Ketamine (10.0 mg/kg) and Xylazine (1.0 mg/km), and Yohimbine (0.125 mg/km) was used to reverse Xylazine (Kreeger et al. 2002). We fit GPS collars (210 – 280 g, Telemetry Solutions, Concord, CA, USA) with timed drop-off mechanisms and degradable cotton spacers along the collar belting on adult-sized bobcats. GPS collars were programmed to record locations on the WS every 5-7 hours and on the FR every 3-4 hours. Bobcats were weighed, sex was recorded, and age was estimated based on tooth development (Crowe 1975), wear, and coloration. Pumas were captured from 2005 – 2011 with the use of hounds and baited cage traps, immobilized with Telazol (5.0 – 9.0 mg/kg), and fit with GPS collars (Lotek, Newmarket, Ontario, Canada; Northstar, King George, VA, USA; Vectronics, Berlin, Germany) programmed to record a location every 5-7 hours on the WS and 3-4 hours on the FR . To increase the duration of time that location data were acquired for adult male pumas on the WS, some individuals were fit with VHF collars (Lotek) and aerial positional locations were obtained approximately every 2 weeks. Pumas were also weighed, fit with eartags, and sex and age were recorded. If scale weights on felids were unavailable at the time of capture, body weight was estimated based on animal size and sex. Body weights generally increased across categories of small females, large females,

small males, and large males. Methods for animal capture were approved by the Colorado State University Animal Care and Use Committee (11-2453A).

Estimating Population Size and Density

Using data from marked and unmarked individuals, we conducted population modeling using a two-step approach: first we estimated the population size and then we used telemetry information of marked individuals to estimate density.

Individually Marking and Identifying Animals

Each bobcat was assigned a unique color combination between the GPS collar and eartags; this information along with the animal's natural pelt pattern was used for identification of marked individuals in photographs obtained from motion-activated cameras. During captures, photographs were taken of the bobcat's head, body, legs, and tail (Heilbrun et al. 2003) to aid in identifying bobcats on motion-activated cameras prior to them being physically captured and marked. Individually marked pumas were identified by evaluating unique collar and eartag characteristics, as well as the proximity of GPS locations to camera sites in relation to photo times. In contrast to bobcats, pumas are typically not individually-identifiable by pelt patterns, thus puma photos from motion-activated cameras obtained prior to their physical capture could not be linked to subsequent photos of individuals after they were marked; we therefore did not include these individual pumas in the marked sample and counted all their photos as unmarked. Photographs of animals that were not physically captured were classified as unmarked individuals.

Mark-Resight Population Size Estimation

To estimate population size ($\widehat{N}$) we used mark-resight techniques and the Poisson log-normal mixed effects model (PNE; McClintock et al. 2009, Alonso 2012, McClintock and White

2012) using the R (R Development Core Team 2014) package RMark (Laake and Rexstad 2013) to construct models in Program MARK (White and Burnham 1999). Mark-resight models use encounter data (e.g., photos from motion-activated cameras) of marked and unmarked animals to estimate $\widehat{N}$ (McClintock and White 2012). We used the PNE mark-resight model because with motion-activated cameras sampling is with replacement and we individually identified marked animals. We satisfied the critical assumption of mark-resight models that the sighting probability of marked individuals was representative of the entire population by marking individuals via physical capture and using a different method (i.e., motion-activated cameras) to resight individuals. Three parameters were estimated in mark-resight PNE models: 1) α_j (alpha): the intercept for mean resighting rate during primary interval *j*; α is similar to capture probabilities in mark-recapture estimators; 2) σ_j (sigma): individual heterogeneity level of resighting during primary interval *j*; and 3) U_j : number of unmarked individuals in the population during primary interval *j* (McClintock and White 2012). If the population is not closed geographically, as was the case in our study, then mark-resight models estimate the super population size ($\widehat{N}^*$), or the number of individuals that used the sampling grids during the period of our camera surveys (McClintock and White 2012).

We considered 3 covariates on the parameters α and σ in our mark-resight models. *Weight* (kg) was included in modeling because we predicted that larger animals would use broader spatial extents (Gompper and Gittleman 1991, Grigione et al. 2002, Ottaviani et al. 2006) and thus be more likely to be photographed because they would be expected to encounter more cameras on a grid. We considered the covariate s*ex* due to potential behavioral differences between males and females, predicting that males would move more than females per day as they searched for mates and defended territories, while females moved less for security and to

provision young (Logan and Sweanor 2001, Riley et al. 2003). However, the covariates *sex* and *weight* were highly correlated (Pearson's correlation > 0.6), where males were consistently larger than females. Due to the potentially confounding interpretation of these variables, we removed *sex* and retained *weight* in our analyses because we believed that *weight* best reflected potential differences in space use (and thus photographic rates) across adult individuals and within gender categories; space use was predicted to increase across small females, large females, small males, and large males. Lastly, time spent on grid for an individual ($TSOG_{indiv}$; see below for calculation) was included because we predicted that the more time an animal spent on the sampling grid, the more likely it was to be photographed. White and Shenk (2001) advised that telemetry data collected during times that were not concurrent with resighting surveys could be used to estimate the time spent on the sampling grid. When this was not possible (e.g., due to collar malfunction), we used the mean value of $TSOG_{indiv}$ across all animals ($TSOG_{pop}$; see below for calculation) for an individual without a unique estimate of $TSOG_{indiv}$, as recommended by Cooch and White (2012, see Chapter 11 Individual Covariates).

Models were created *a priori* and compared using Akaike's Information Criteria corrected for small sample size (AIC_c; Burnham and Anderson 2002). To test for individual heterogeneity (i.e., variation in resighting rates among individuals), models with no individual heterogeneity (i.e., $\sigma=0$) were compared to models with individual heterogeneity (i.e., σ estimated). We created a candidate model set (with 20 models per set) that included all possible additive combinations of w*eight*, $TSOG_{indiv}$, *weight* + $TSOG_{indiv}$, and constant structures for α and σ, and also considered models with $\sigma=0$. We fit this model set to data from each grid, as well as both grids combined for each study area (Appendices Tables 1 – 12). When using covariates in mark-resight models, model convergence is sensitive to initial values for

parameters; therefore, we first ran a simple model where all parameters were constant ($\alpha(.)\sigma(.)U(.)$), and then used these parameter estimates as initial starting values in models with covariates (McClintock 2012). We report model-averaged estimates of the population size (the derived parameter $\widehat{N}$), to incorporate model uncertainty (Burnham and Anderson 2002). In addition, we model averaged estimates of covariates (Lukacs et al. 2010) and calculated variable importance values for covariates across all models (Burnham and Anderson 2002, Anderson 2008).

Estimating Density Using $TSOG_{pop}$

We used model-averaged estimates of population size ($\widehat{N}$) from the mark-resight models and the proportion of time spent on the grid by the sampled population ($TSOG_{pop}$; referred to as $\bar{p}$ by White and Shenk 2001) to estimate population density (number of individuals per area, i.e., 100 km^2) for our study areas (White and Shenk 2001). First, TSOG for each individual ($TSOG_{indiv}$; referred to as p_i by White and Shenk 2001) is estimated by dividing the number of locations on the grid (g_i) by the total number of locations for the individual during the time period of interest (G_i), or formally $TSOG_{indiv} = g_i / G_i$. Next, the mean of $TSOG_{indiv}$ across all telemetered individuals ($TSOG_{pop}$) and the estimate of $\widehat{N}$ are used to estimate density as: $\widehat{D} = (\widehat{N} * TSOG_{pop}) / A$, where A is the area of the sampling grid. The numerator of this expression represents the number of individuals that used the grid during the primary period multiplied by the proportion of time individuals were on the grid; thus the abundance estimate is adjusted to the area of the grid. The variance of $\widehat{D}$ is estimated as $\mathrm{Var}(\widehat{D}) = (\widehat{N}^2\widehat{\mathrm{Var}}(\mathrm{TSOGpop}) + \mathrm{TSOGpop}^2\,\widehat{\mathrm{Var}}(\widehat{N}))/A^2$ (White and Shenk 2001), which was used to estimate standard errors. Although photos of pumas that were physically captured (and thus marked) partway through the camera surveys were classified as unmarked animals for estimating $\widehat{N}$, as described above, their

telemetry data were used to estimate $TSOG_{pop}$. In addition, if $TSOG_{indiv}$ was unavailable for a felid (e.g., due to collar malfunction) and a mean value of $TSOG_{indiv}$ was used in mark-resight models, as described above, these values were excluded from estimation of $TSOG_{pop}$ for density.

White and Shenk (2001) cautioned that TSOG techniques can lead to estimates of $\widehat{D}$ that are biased high if animals spending little time on the grid are less likely to be captured than animals that spend most of their time on the grid. In our study, we physically captured animals across the entirety of the sampling grids, including areas along the edge of the grid and areas towards the interior of the grid, as well as off of the sampling grids. In addition, due to the relatively large home ranges of bobcats and pumas, animals captured towards the interior of the grids often spent considerable time off of the grids as well. Thus, the potential for this bias was minimized. In addition, we accounted for individual variation in the resighting rate that is used to estimate abundance in mark-resight models by including the covariate $TSOG_{indiv}$.

Occupancy Modeling

Because of the relationship between population density and detection/non-detection data, occupancy modeling might be appropriate to use as a surrogate for abundance (MacKenzie and Nichols 2004, MacKenzie et al. 2006, Noon et al. 2012). Although more coarse compared to population density, occupancy (Ψ; the proportion of the landscape used by the species) and species detection probability (p; the probability of detecting a species given that it was present at a site) are related to the distribution of abundance across the area of interest (Royle and Nichols 2003, Royle et al. 2005). Therefore, we predicted that occupancy and detection probability would follow similar patterns as described for population density in relation to urbanization. Animals may exhibit high estimates of occupancy across a heterogeneous landscape (indicating use of many different sites), but the relative use of sites can vary widely depending upon how

animals select for habitat characteristics; this argument is the foundation for similar studies of resource selection where animals may occur across broad spatial extents (i.e., occupy most of the landscape), but select for or against specific landscape characteristics depending on species-habitat relationships (e.g., Manly et al. 2002). Although many factors influence detection probability and it is often considered a nuisance parameter in occupancy models (MacKenzie et al. 2006), detection probability can be evaluated using covariates in occupancy models to understand the relative use of sites and local population abundance (Royle and Nichols 2003, Royle et al. 2005). We evaluated the behavioral response of animals to landscape features by investigating how detection probability, which reflected the frequency of use of an area by the species, varied in relation to habitat covariates. We assumed that species would exhibit higher estimates of detection probability at preferred sites (and thus be more likely to use these areas) and lower estimates of detection probability at less suitable sites, as explained by habitat covariates. Inference from motion-activated cameras is in relation to the movement behavior of animals when traveling past sampling locations.

We used single-species single-season occupancy models to estimate occupancy and detection probability (MacKenzie et al. 2006) for both bobcats and pumas in each study area across five sampling occasions, with each sampling occasion occurring over 22 days on the WS and 18 days on the FR. We used the R (R Development Core Team 2014) package RMark (Laake and Rexstad 2013) to construct occupancy models in Program MARK (White and Burnham 1999). We used a three-step approach to construct models in our occupancy analysis. First, we evaluated whether survey effort influenced detection probability at our two study areas. Although uncommon, not all cameras operated for the same number of days due to camera malfunction, expired batteries, full memory cards, vandalism, or theft of cameras. We thus

calculated a time varying *effort* covariate for each camera location across the five sampling occasions; this covariate represented the proportion of days the camera was operational during a given sampling occasion (e.g., if a camera operated 15 out of 18 days during a sampling occasion, then effort equaled 0.83 for this occasion). Using the global model structure on the occupancy parameter (see next section), we fit a model with constant detection probability (p(.)) and compared it to a model where detection probability varied with e*ffort* (p(Effort)). If p(Effort) was more supported than p(.) based on AIC_c scores, then p(Effort) was included in all subsequent models.

Second, two covariates (*grid* and *human development*) were used to model potential variation in occupancy and detection probability among sites (i.e., camera locations). The covariate *grid* compared camera sites between either exurban and wildland areas (on the WS) or wildland-urban interface and wildland areas (on the FR). The covariate *human hevelopment* characterized the amount of human influence (Lewis et al. 2011) associated with each camera location. To determine an appropriate human development value for each camera location, we created a human development layer where each human occurrence point (HOP; residence or structure) in the study areas was digitized as a point using ArcMap10 geographic information system (GIS) software (ESRI, Redlands, CA, USA) from color orthophotos. Using Arc Toolbox in ArcMap10, we fit a Gaussian kernel over each HOP, where the density, or influence, was greatest directly at the point of interest and decreased out to a specified radius of a circle; radii ranged from 100 – 1000 m on the WS and 100 – 1500 m on the FR. In GIS, each camera location was intersected with the cumulative kernel density of human development across each radius. For occupancy modeling analyses, each human development input variable was standardized by subtracting the sample mean from the input variable values and dividing by the

standard deviation (Schielzeth 2010). To determine which spatial scale of human development was appropriate for each species and study area, we compared univariate models where detection probability was modeled as a function of the human development covariate across radii, and used AIC_c model ranking to determine the best scale. Based on this approach, we used a radius of 200m for bobcats and pumas on the WS and 1300m for bobcats and 300m for pumas on the FR.

Finally, we evaluated the influence of our two covariates (*grid* and *human development*) on both occupancy and detection probability by fitting a candidate model set consisting of all possible combinations of *grid*, *human development*, both, or neither (constant) structures (16 models) to data for each species and study area (Appendices Tables 13 – 16). We report model-averaged parameter and covariate estimates and calculated variable importance values for each covariate (Burnham and Anderson 2002, Lukacs et al. 2010). To obtain estimates of occupancy and detection probability for each grid, we model averaged results for models that included the covariate g*rid* on both parameters.

Because the availability of prey is a potential mechanism influencing felid density (Logan and Sweanor 2001, Ferguson et al. 2009, Ruth and Murphy 2010) across study areas (i.e., the ideal free distribution; Fretwell 1972), we estimated the occupancy and detection probabilities using camera data for the primary prey species of bobcats (cottontail rabbits *Sylvilagus spp.*) and pumas (mule deer *Odocoileus hemionus* and elk *Cervus elaphus*) (Sunquist and Sunquist 2002) for each grid, using methods as explained above for felids evaluating Ψ(Grid) p(Grid) models.

RESULTS

Photos from Motion-Activated Cameras

All motion-activated cameras on the WS and FR obtained at least 1 photograph of a felid during our surveys. On the WS, we obtained 185 photographs of bobcats across 38 sites and 80 photographs of pumas across 23 sites during 113 days (Table 1). On the FR, we obtained 150 photographs of bobcats across 32 sites and 96 photographs of pumas across 36 sites during 92 days (Table 1).

Animal Capture and Telemetry Data

We physically captured and marked 20 bobcats and 9 pumas on the WS and 16 bobcats and 10 pumas on the FR (Table 1). $TSOG_{indiv}$ ranged from 0.08 - 1.0 for bobcats and 0.08 - 0.73 for pumas on the WS and 0.06 - 0.99 for bobcats and 0.03 - 0.80 for pumas on the FR. $TSOG_{pop}$ was similar for felids between grid areas on the FR, and $TSOG_{pop}$ was lower for bobcats and pumas on the exurban grid compared to the wildland grid on the WS (Table 1). Bobcats spent more time on the WS wildland grid compared to FR wildland grid, which is consistent with smaller bobcat home ranges on the WS compared to the FR (unpublished data).

Population Density, Occupancy, and Detection

Consistent with predictions of reduced habitat suitability in low-density urban development, on the WS, population density appeared to be lower for bobcats and pumas in exurban development compared to wildland habitat, although 95% confidence intervals overlapped. Occupancy estimates were similar between the two grids for each species (Table 1, Figure 2a). Counter to predictions regarding home-range pile-up, population density and occupancy were not greater for bobcats and pumas along the wildland-urban interface compared to wildland habitat on the FR (Table 1, Figure 2b). Detection probability for bobcats tended to

be greater on grids influenced by urbanization compared to wildland grids (Figure 2). For pumas, detection probability on the WS was lower on the exurban grid compared to wildland grid and was similar between grids on the FR (Figure 2).

Covariates in Mark-Resight and Occupancy Models

For some mark-resight model sets, larger individuals that spent more time on the sampling grid exhibited the highest resighting rate and were thus photographed more often (Table 2, Appendices Tables 1 – 12). These relationships were strongest for felids on the WS when both grid areas were evaluated collectively; both $TSOG_{indiv}$ and *weight* exhibited positive relationships with the mean resighting rate (α), where 95% confidence intervals did not overlap 0 (Table 2, Appendices Tables 1 – 12). $TSOG_{indiv}$ was generally a more important covariate than weight (based on variable importance values), although both covariates helped explain mean resighting rates in models (Table 2). Models where the individual heterogeneity level of resighting (σ) was fixed to 0 were generally the most supported (Appendices Tables 1 – 12).

In occupancy models, covariates were generally unsupported when estimating occupancy, but were supported when estimating detection probability (Table 3; Appendices Tables 13 - 16). Species occurrence across sites was fairly constant in both study areas, as the top model never included occupancy structures with either of our two covariates (Table 3; Appendices Tables 13 – 16). For detection probability, the covariate e*ffort* was not supported on the WS (bobcats: Ψ(Grid) p(.) AIC_c = 280.96, Ψ(Grid) p(Effort) AIC_c = 282.58; pumas: Ψ(Grid) p(.) AICc = 217.90, Ψ(Grid) p(Effort) AIC_c = 220.24), but was supported on the FR (Appendices Tables 15 and 16). On the FR, there was a positive relationship between e*ffort* and detection probability for both bobcats and pumas (Table 3, Appendices Tables 15 and 16); the probability of detecting felids increased with the number of days that a camera operated during a sampling

occasion. For both bobcats and pumas on the WS and FR, detection probability and *human development* were negatively related; felids were less likely to be detected as the influence of human development increased at a site (Table 3, Appendices Tables 13 – 16). Parameter estimates for *human development* evaluating detection probability for pumas demonstrated a stronger relationship in top models on the WS (β = -0.82, se = 0.45, model weight = 0.24) and FR (β = -0.34, se = 0.21, model weight = 0.20) compared to the model averaged parameter estimates (Table 3; Appendices Tables 14 and 16). For bobcats on the WS and FR, parameter estimates in top models were generally consistent with model averaged parameter estimates (Table 3; Appendices Tables 13 and 15). Lastly, detection probability appeared to vary by grid for bobcats, but not pumas (Figure 2), based on the presence and absence of the covariate *grid* in top models (Appendices Tables 13 – 16).

Occupancy of Prey Species

Occupancy of important prey for bobcats (cottontail rabbits) and pumas (mule deer) was consistently high across study areas. On the WS, occupancy and detection probability of cottontail rabbits and mule deer were similar between the exurban and wildland grids (Table 4). On the FR, occupancy and detection probability of cottontail rabbits was similar between grids and mule deer occupancy was slightly lower on the wildland-urban interface grid compared to the wildland grid (Table 4). On both the WS and FR, elk exhibited lower occupancy on the exurban and wildland-urban interface grids, respectively, compared to the wildland grid and detection probability was similar among all grid areas (Table 4).

DISCUSSION

Our study indicates that low-density residential development influenced wild felid populations more than habitat adjacent to a major wildland-urban interface. Point estimates of population density were lower for bobcats and pumas in exurban development compared to wildland habitat, suggesting reduced habitat quality, whereas population density for both felids appeared more similar between wildland-urban interface (WUI) and wildland habitat, in contrast to predictions of home-range pile-up and density inflation along impermeable boundaries (Riley et al. 2006). In addition, the occupancy of important felid prey (cottontail rabbit and mule deer) was generally high and similar between sampling grids, suggesting that felid population densities were not substantially altered by availability of these prey within study sites.

Many mechanisms associated with urbanization can influence population characteristics of animals (Shochat et al. 2006), including altered movement patterns. Populations completely surrounded by movement barriers may reach higher densities compared to unbounded populations (Krebs et al. 1969, Adler and Levins 1994). Further, the home-range pile-up hypothesis predicts that populations where animal movement is only partially restricted will also reach higher densities in habitat adjacent to an anthropogenic barrier (Riley et al. 2006). Research testing these predictions, especially for wild felids in urban systems, is limited. Home-range pile-up was reported for a bobcat population adjacent to a major highway in southern California (Riley et al. 2006), but other urban bobcat studies have not found evidence consistent with this hypothesis and report that population densities of bobcats often are not higher in urban fragments and are lower when compared to more unbounded populations in wildland areas (Lembeck and Gould 1979, Ruell et al. 2009, Riley et al. 2010). Further, although movement patterns, habitat selection, and mortality factors of pumas have been evaluated in relation to

urbanization (Beier et al. 2010, Burdett et al. 2010, Wilmers et al. 2013), few studies have estimated the density of pumas across different levels of urbanization (Beier et al. 2010).

Although our study did not find support for the home-range pile-up hypothesis for either bobcat or puma populations associated with a major urban barrier, we provide several considerations when interpreting our results. First, the related fence-effect hypothesis states that population density will initially increase due to restricted movement, but that density will eventually decrease due to limited resources (Krebs et al. 1969). The wildland-urban interface of Boulder, CO has existed for more than a century. It is possible that population density has already reached an equilibrium resulting from this landscape barrier. Second, the wildland-urban interface of Boulder occurs over the length of 14 km. Although this barrier is mostly impermeable to animal movement for its entire stretch, perhaps a longer and more significant barrier is necessary to impact population characteristics of felids. Third, negative ecological impacts related to edge effects along the urban interface (Murcia 1995), such as mortality from people, vehicles, and disease, could suppress population densities. We did not have detailed information about animal mortality, but other studies have reported greater mortality and reduced fitness of wild felids from anthropogenic factors near urban areas and human development (Beier et al. 2010, Burdett et al. 2010). Fourth, increased densities may only be observed for specific age and sex classes (e.g., adult females; Riley et al. 2006) or during certain times of the year (e.g., winter). Our approach for estimating felid densities was not able to differentiate among different age and sex classes in the unmarked population and we thus evaluated all adult-sized individuals collectively during a single season. Lastly, populations that are bounded on only one side of their spatial extent, such as those along an urban interface in our study area, might not experience elevated population density because dispersing animals have the option to leave the

population. Thus, a single linear barrier might not produce a sufficient barrier to dispersal to alter population density; abnormally high population densities might only occur in landscapes that are completely isolated, as predicted by the fence-effect or island syndrome hypotheses, where animal dispersal is impossible or substantially diminished (Krebs et al. 1969, Adler and Levins 1994).

Another mechanism that can influence populations of animals is disturbance from human activities associated with residential development, which can reduce habitat quality. Our study demonstrated that exurban and rural residential development decreased population density of both bobcats and pumas compared to wildland habitat. Thus, although low-density development may increase landscape heterogeneity and potentially carnivore food along ecotones and edges (Murcia 1995, Irwin and Bockstael 2007), anthropogenic disturbance associated with such development across broad spatial extents appears to degrade habitat suitability and reduce wild felid density. Both bobcats and pumas spent less time on the exurban sampling grids compared to wildland areas (based on GPS collar data) and behaviorally both species were less likely to be observed at sites with greater influence of residential development compared to undeveloped sites (based on detection probability in relation to human residences). However, both felids used natural areas intermixed within exurban development, and the exurban grid was adjacent to expansive wildland areas that supported felid populations, both of which likely mitigated the impacts of exurban development on felid populations in these areas. Consistent with our findings, pumas in urbanized California used areas of exurban development less than expected (Burdett et al. 2010). Further, pumas that use habitat near humans and development have a higher risk or mortality (Burdett et al. 2010, Wilmers et al. 2013), which could reduce the density of populations in such areas. Given that exurban residential development is the fastest growing

form of urbanization (Brown et al. 2005, Nelson and Sanchez 2005), it is important to consider the ecological impacts associated with this type of anthropogenic disturbance.

Although point estimates for population densities of felids were lower in exurban development, estimates of occupancy for both bobcats and pumas were more similar between wildland areas and habitat associated with residential development, which was inconsistent with our predictions. Studies of presence-absence (Gaston et al. 2000) and occupancy (MacKenzie and Nichols 2004, MacKenzie et al. 2006, Temple and Gutiérrez 2013) of animals have reported a positive relationship between abundance and occurrence. Although this relationship is intuitive, it likely is valid only up to a certain threshold and therefore non-linear (Freckleton et al. 2005, Noon et al. 2012). For example, occupancy estimates will increase only if additional sites are used as population densities increases. Alternatively, if the population size grows within sites already occupied, density will increase, but occupancy probabilities will remain unchanged; in such cases, occupancy probabilities may asymptote at 1.0 at moderate to high population densities. Unless individuals are territorial or a site can be defined to limit the number of individuals that are likely to occupy it (MacKenzie and Nichols 2004), the ability of occupancy to track total abundance within an area is limited. Further, even for large changes in population size, intensive sampling is necessary to observe changes in occupancy (Ellis et al. 2014). Thus, it has been argued that detection-non-detection data can have little power to detect changes in abundance in many systems (Strayer 1999, Pollock 2006). This appeared to be the case in our study and likely occurred because both species will use habitat components that are less preferred (and thus occupy a site), but frequent these areas less than habitat of higher suitability (see discussion on detection probability below). Species that occur at low densities but have wide-ranging movement patterns will likely exhibit high estimates of occupancy over longer

sampling occasions because of the species' ability to visit much of the landscape (MacKenzie and Royle 2005). Thus, occupancy appears to be a relatively poor metric to evaluate differences in population densities in our system.

Detection probability is another metric used to evaluate the behavior or density of animals relative to landscape characteristics. It is assumed that abundance is related to species detection probability (Royle and Nichols 2003, Royle et al. 2005) or detection rate (Carbone et al. 2001); species detection probability should correspond to local abundance because more animals are available to be detected. In addition, animals would be expected to demonstrate higher detection probabilities in habitat of higher suitability because they will likely frequent these areas more often. In our study, detection probability of bobcats and pumas appeared to be a more sensitive metric than occupancy, but sometimes produced unexpected results. For example, as predicted, across study areas, both felids were less likely to be detected as the amount of human influence from residential development increased; thus, although felids would use these sites, they visited developed areas less often compared to undeveloped sites. However, despite this, bobcats unexpectedly exhibited higher overall detection probabilities in both exurban and wildland-urban interface grids compared to wildland grids. This likely occurred because animals in urbanized landscapes had fewer options to travel due to anthropogenic barriers to movement (e.g., human residences, roads, urban barriers) and were thus funneled along more restrictive movement corridors. Our sampling technique of placing motion-activated cameras within these key movement corridors likely increased our detection of animals. In wildland habitat, more movement options were likely available to animals throughout the landscape. In contrast to bobcats, and consistent with predictions, detection probability for pumas was lower in exurban habitat compared to wildland areas (Figure 2). Thus, bobcats and

pumas might exhibit different movement behaviors when using urbanized landscapes. For carnivores, it is recommended that sampling occur along high probability travel routes to obtain sufficient data of animals (Karanth et al. 2010). It is important to consider, however, that sampling schemes that aim to increase detection of animals by directed placement of sampling devices can potentially lead to unexpected results that initially might appear counter-intuitive and should be interpreted carefully.

Densities of urban-adapted species often are greater in urban systems compared to wildland habitat due to multiple ecological factors (Gehrt et al. 2010). For example, increased forage near and within urban areas can increase population densities for species such as raccoons (*Procyon lotor*) (Hadidian et al. 2010) and red fox (*Vulpes vulpes*) (Soulsbury et al. 2010). In our study, however, occupancy of important felid prey (i.e., cottontail rabbits and mule deer) was high and generally similar among exurban, wildland-urban interface, and wildland areas, suggesting availability of these prey did not contribute to differing population characteristics of felids among sampling areas. In contrast, the occupancy of elk was substantially lower in exurban and wildland-urban interface habitat compared to wildland areas, suggesting reduced availability of elk near residential developments. As demonstrated for felids in our study, occupancy might not always be a sensitive index for abundance, so occupancy of prey might not reflect their relative density. In some cases, detection probability of prey varied between grids for a species (e.g., mule deer exhibited greater detection probability in exurban habitat compared to wildland areas), indicating potential differences in abundance or use. In addition, both bobcats and pumas exhibit a varied diet (Sunquist and Sunquist 2002) and it is unclear how densities across the prey community, which we were not able to measure, were impacted by urbanization and how this might have affected felid populations. Other factors that could

influence the population density of felids that we did not evaluate in our study include the effect of individuals of varying competitive abilities (i.e., ideal despotic distribution; Fretwell 1972) and body size (i.e., competitive units; Milinski 1988). Our analyses also did not consider how urbanization influenced intra- or interspecific competition in felid populations, although competition can substantially influence population density of animals and community structure (Crooks and Soulé 1999).

Our research evaluating medium- and large-sized carnivores associated with varying levels of urbanization provides important information about the conservation of wildlife populations associated with urban and exurban residential development. Wildland habitat adjacent to urban areas can effectively support bobcat and puma populations and thus management strategies that conserve habitat associated with urbanized landscapes can potentially play important roles in the persistence of carnivore populations. For example, our estimate of puma population density in wildland-urban interface habitat are consistent with, and indeed on the higher end of, the range of reported estimates of puma population densities in other systems (Quigley and Hornocker 2009). In addition, our results indicate that the conversion of wildland habitat to low-density (exurban and rural) residential development will likely reduce population density for some native species, such as bobcat and puma, even though these forms of urbanization are permeable to animal movement and support populations of prey species. Because animals will use habitat that is associated with human residences, there is greater potential in these areas for human-wildlife conflict, disease transmission among wildlife, humans, and domestic animals, and reduced fitness compared to animals living in wildland habitat (Hansen et al. 2005, Bradley and Altizer 2007, McDonald et al. 2008). Thus, our study indicates that the conservation of medium- and large-sized carnivores in landscapes associated

with urbanization will likely be most successful if large areas of wildland habitat are maintained, even in close proximity to residential and urban areas, and wildland habitat is not converted to low-density residential development.

Table 1. Summary of marked individuals, photos, population size, TSOG (time spent on grid), and density for bobcats and pumas in relation to exurban and wildland grids on the Western Slope (WS) in 2009 and wildland-urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado.

Study			# Marked Animals	# Marked	# Photos Per Marked Individual				# Unmarked			Area	Density (se)
Area	Species	Grid Areas	Detected and Present	Photos	Mean	Median	Range	Alpha (se)[a, b]	Photos	N (se)[b]	TSOG (se)	(km^2)	(# / 100 km^2)
WS	Bobcat	Exurban	9 / 11	42	3.82	3.00	0 - 15	2.62 (0.57)	56	25.55 (3.00)	0.50 (0.12)	80	15.96 (2.01)
WS	Bobcat	Wildland	8 / 10	24	2.40	1.50	0 - 7	2.25 (0.56)	49	30.32 (5.61)	0.63 (0.10)	80	23.99 (2.87)
WS	Bobcat	Both Grids	17 / 20	66	3.30	2.50	0 - 15	2.61 (0.45)	105	52.62 (6.25)	0.59 (0.08)	160	19.37 (3.33)
WS	Puma	Exurban	3 / 4	17	4.25	5.00	0 - 7	4.25 (1.03)	22	9.06 (1.63)	0.12 (0.02)	80	1.34 (0.30)
WS	Puma	Wildland	6 / 6	33	5.50	3.00	2 - 19	3.91 (1.25)	8	7.35 (0.77)	0.30 (0.13)	80	2.76 (1.04)
WS	Puma	Both Grids	8 / 9	50	5.56	4.00	0 - 26	3.52 (0.77)	30	14.37 (1.62)	0.25 (0.09)	160	2.23 (0.76)
FR	Bobcat	WUI	5 / 8	25	3.13	2.50	0 - 13	1.71 (0.99)	56	23.07 (8.20)	0.53 (0.13)	80	15.26 (3.14)
FR	Bobcat	Wildland	8 / 9	20	2.22	1.00	0 - 6	2.19 (0.51)	49	30.84 (5.91)	0.52 (0.11)	80	19.84 (2.71)
FR	Bobcat	Both Grids	13 / 16	45	2.81	2.50	0 - 13	2.05 (0.56)	105	55.07 (11.41)	0.56 (0.08)	160	19.23 (4.69)
FR	Puma	WUI	4 / 4	28	7.00	7.00	1 - 13	7.00 (1.32)	22	7.07 (0.88)	0.33 (0.13)	80	2.94 (1.21)
FR	Puma	Wildland	5 / 5	29	5.80	6.00	2 - 10	5.80 (1.08)	17	7.58 (0.76)	0.36 (0.13)	80	3.40 (1.26)
FR	Puma	Both Grids	9 / 9	57	6.33	6.00	1 - 13	6.24 (0.92)	39	14.74 (1.27)	0.34 (0.09)	160	3.17 (0.89)

[a] Alpha is the mean resighting rate estimated from mark-resight models (see Methods).

[b] Model-averaged estimates and unconditional standard errors (se).

Table 2. Summary of covariate estimates from mark-resight models for bobcats and pumas in relation to exurban and wildland grids on the Western Slope (WS) in 2009 and wildland-urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado. α = alpha (mean resighting rate); σ = sigma (individual heterogeneity level); TSOG = time spent on grid for individual animal based on telemetry locations; Weight = weight (kg) of animal; β = model averaged (based on AICc weights) parameter estimate with associated standard error; VIV = variable importance value based on sum of AICc weights. See text for further description of parameters. See Appendices Tables 1 – 12 for complete set of tables reporting results of individual models and covariate estimates for mark-resight models.

			α				σ			
			TSOG		Weight		TSOG		Weight	
Study Area	Species	Grid Areas	β (se)	VIV	β (se)	VIV	β (se)	VIV	β (se)	VIV
WS	Bobcat	Exurban	2.45 (0.52)	1.00	0.14 (0.07)	0.63	na	0.00	na	0.00
WS	Bobcat	Wildland	0.32 (0.41)	0.27	0.01 (0.07)	0.10	na	0.02	na	0.02
WS	Bobcat	Both Grids	1.60 (0.48)	0.90	0.10 (0.07)	0.54	0.50 (1.71)	0.15	0.08 (0.34)	0.12
WS	Puma	Exurban	0.00 (0.00)	0.00	0.00 (0.00)	0.00	na	0.00	na	0.00
WS	Puma	Wildland	0.19 (0.35)	0.07	0.03 (0.01)	0.54	0.00 (0.00)	0.00	0.00 (0.00)	0.00
WS	Puma	Both Grids	2.07 (0.58)	0.83	0.05 (0.01)	0.85	0.05 (0.28)	0.02	0.00 (0.01)	0.06
FR	Bobcat	WUI	0.19 (0.47)	0.08	-0.01 (0.08)	0.03	0.01 (0.13)	0.02	0.00 (0.04)	0.02
FR	Bobcat	Wildland	0.05 (0.25)	0.11	0.00 (0.04)	0.09	0.00 (0.22)	0.01	0.00 (0.05)	0.01
FR	Bobcat	Both Grids	0.24 (0.44)	0.23	0.00 (0.05)	0.13	0.00 (11.46)	0.13	-0.04 (11.45)	0.21
FR	Puma	WUI	0.00 (0.00)	0.00	0.00 (0.00)	0.00	0.00 (0.00)	0.00	0.00 (0.00)	0.00
FR	Puma	Wildland	0.01 (0.10)	0.01	0.00 (0.00)	0.01	0.00 (0.00)	0.00	0.00 (0.00)	0.00
FR	Puma	Both Grids	0.18 (0.30)	0.21	0.00 (0.00)	0.08	-0.11 (0.39)	0.03	0.00 (0.01)	0.01

Table 3. Summary of covariate estimates from occupancy models for bobcats and pumas on the Western Slope (WS) in 2009 and the Front Range (FR) in 2010, Colorado. Ψ = occupancy (proportion of the landscape used by the species), p = detection probability (the probability of detecting a species given that it was present at a site); Grid = covariate comparing urban (=0) and wildland (=1) grids; HumDev = kernel density human development covariate; Effort = time varying survey effort covariate; β = model-averaged (based on AICc weights) parameter estimate with associated standard error; VIV = variable importance value based on sum of AICc weights. See text for further description of parameters. See Appendices Tables 13 – 16 for complete set of tables reporting results of individual models and covariate estimates for occupancy models.

		Ψ				p					
		Grid		HumDev		Effort		Grid		HumDev	
Study Area	Species	β (se)	VIV	β (se)	VIV	β (se)	VIV	β (se)	VIV	β (se)	VIV
WS	Bobcat	na	0.30	na	0.21	na	na	-0.75 (0.29)	0.90	-0.29 (0.15)	0.79
WS	Puma	0.02 (0.35)	0.22	-0.20 (0.48)	0.36	na	na	0.14 (0.24)	0.32	-0.44 (0.38)	0.57
FR	Bobcat	0.27 (0.64)	0.27	-0.01 (0.24)	0.20	1.81 (1.04)	0.97	-0.48 (0.30)	0.63	-0.43 (0.19)	0.82
FR	Puma	na	0.36	na	0.34	1.70 (1.07)	0.92	-0.04 (0.14)	0.22	-0.17 (0.15)	0.51

Table 4. Estimates of occupancy and detection probability for prey species of bobcat (cottontail rabbit) and pumas (mule deer and elk) on exurban and wildland grids on the Western Slope (WS) in 2009 and wildland-urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado. Ψ = occupancy (proportion of the landscape occupied by the species), p = detection probability (the probability of detecting a species given that it was present at a site).

		Ψ				p			
Study		Exurban		Wildland		Exurban		Wildland	
Area	Species	Estimate (se)	95% CI	Estimate (se)	95% CI	Estimate (se)	95% CI	Estimate (se)	95% CI
WS	Cottontail Rabbit	1.00 (0.00)	1.00 - 1.00	0.85 (0.08)	0.62 - 0.95	0.89 (0.03)	0.81 - 0.94	0.85 (0.04)	0.75 - 0.91
WS	Mule Deer	0.95 (0.05)	0.70 - 0.99	0.92 (0.07)	0.65 - 0.99	0.67 (0.05)	0.57 - 0.76	0.54 (0.06)	0.44 - 0.65
WS	Elk	0.39 (0.13)	0.19 - 0.65	0.75 (0.14)	0.42 - 0.92	0.36 (0.09)	0.20 - 0.55	0.33 (0.07)	0.21 - 0.48
WS	Mule Deer and Elk	0.95 (0.05)	0.71 - 1.00	0.96 (0.05)	0.69 - 1.00	0.71 (0.05)	0.61 - 0.80	0.64 (0.05)	0.53 - 0.73
		WUI		Wildland		WUI		Wildland	
		Estimate (se)	95% CI	Estimate (se)	95% CI	Estimate (se)	95% CI	Estimate (se)	95% CI
FR	Cottontail Rabbit	0.66 (0.11)	0.43 - 0.83	0.60 (0.11)	0.38 - 0.80	0.58 (0.06)	0.45 - 0.69	0.65 (0.06)	0.52 - 0.76
FR	Mule Deer	0.71 (0.10)	0.47 - 0.86	1.00 (0.00)	1.00 - 1.00	0.61 (0.06)	0.49 - 0.72	0.73 (0.04)	0.63 - 0.81
FR	Elk	0.28 (0.11)	0.12 - 0.54	0.61 (0.13)	0.35 - 0.81	0.36 (0.11)	0.18 - 0.59	0.38 (0.08)	0.25 - 0.53
FR	Mule Deer and Elk	0.75 (0.10)	0.52 - 0.89	1.00 (0.00)	1.00 - 1.00	0.66 (0.06)	0.55 - 0.76	0.78 (0.04)	0.69 - 0.85

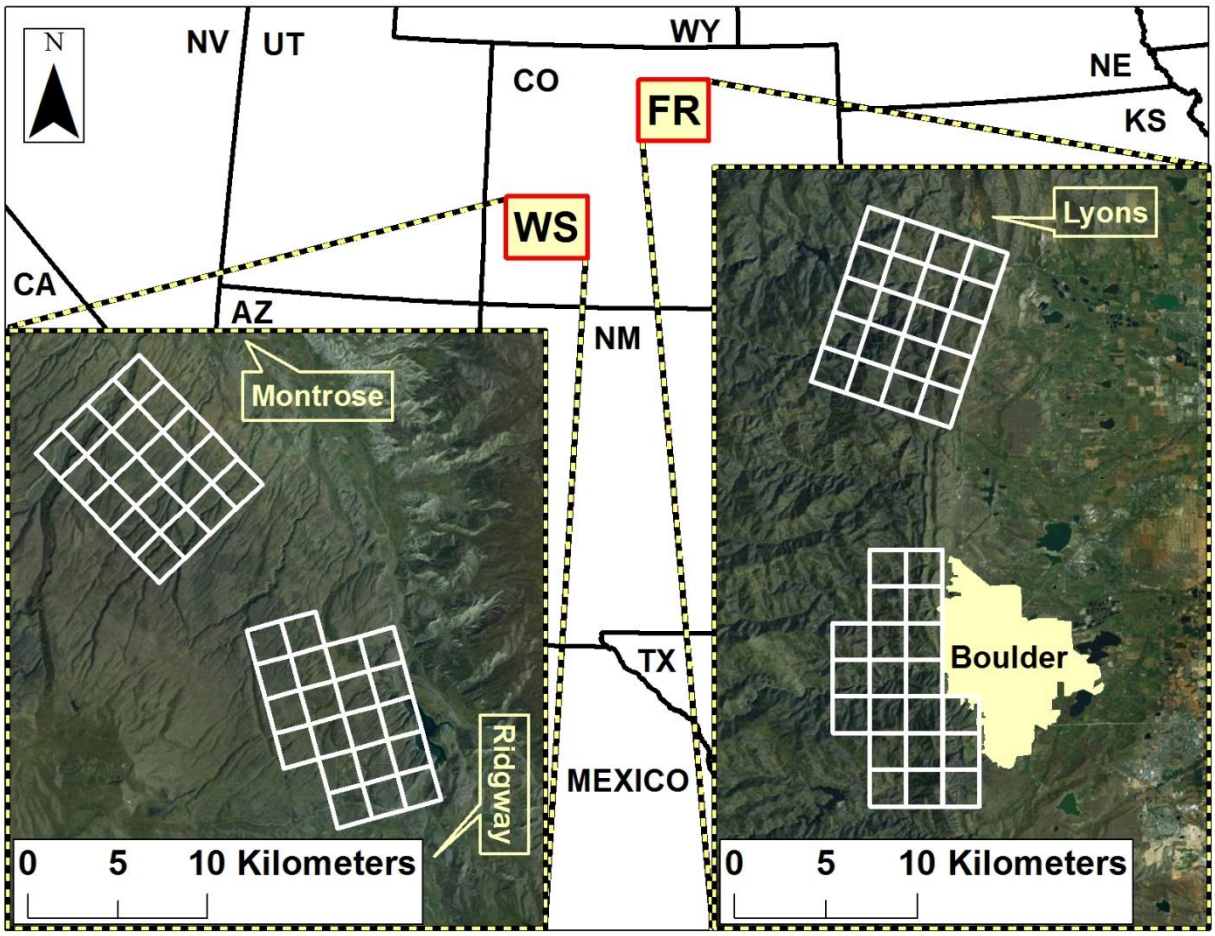
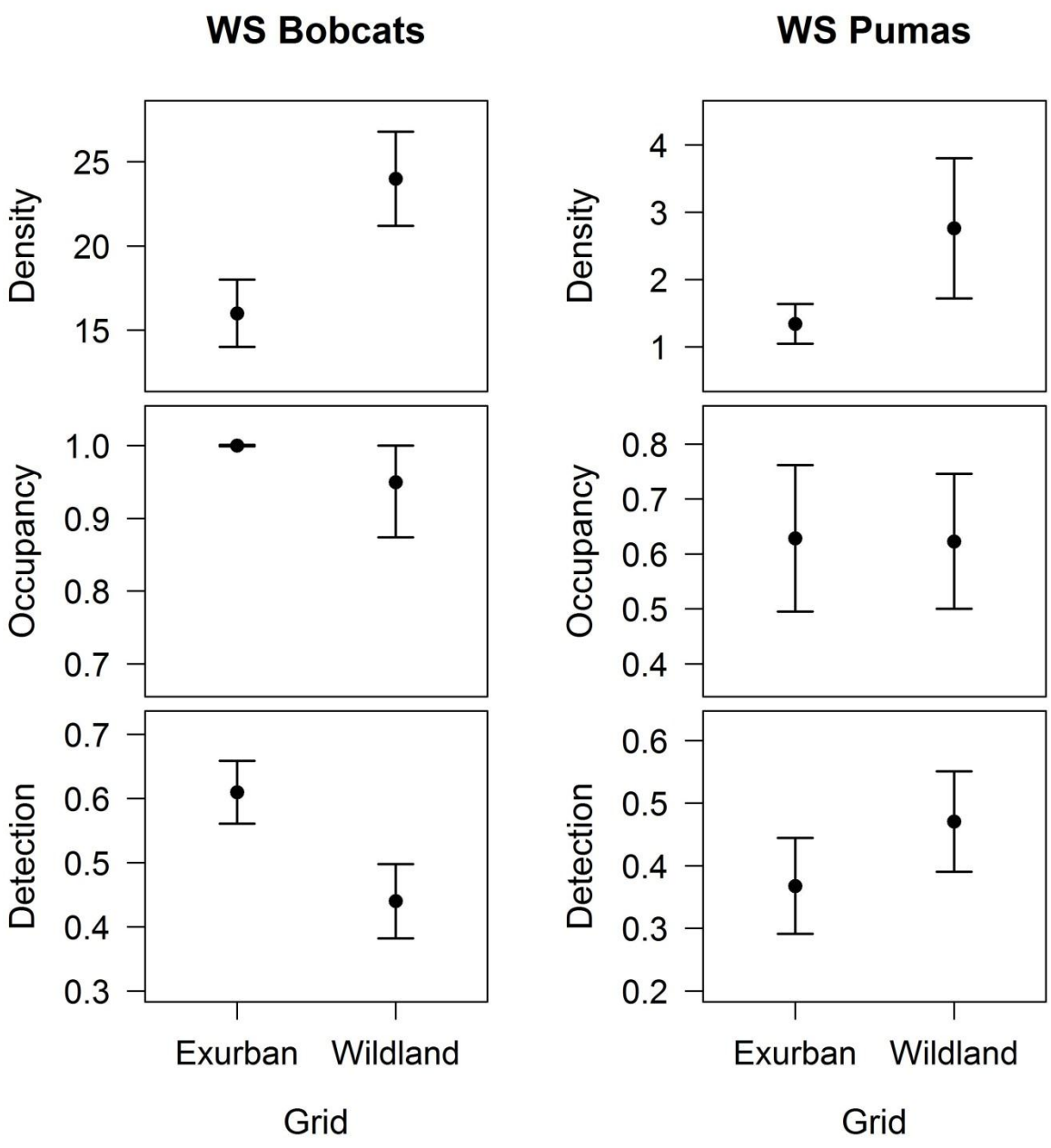
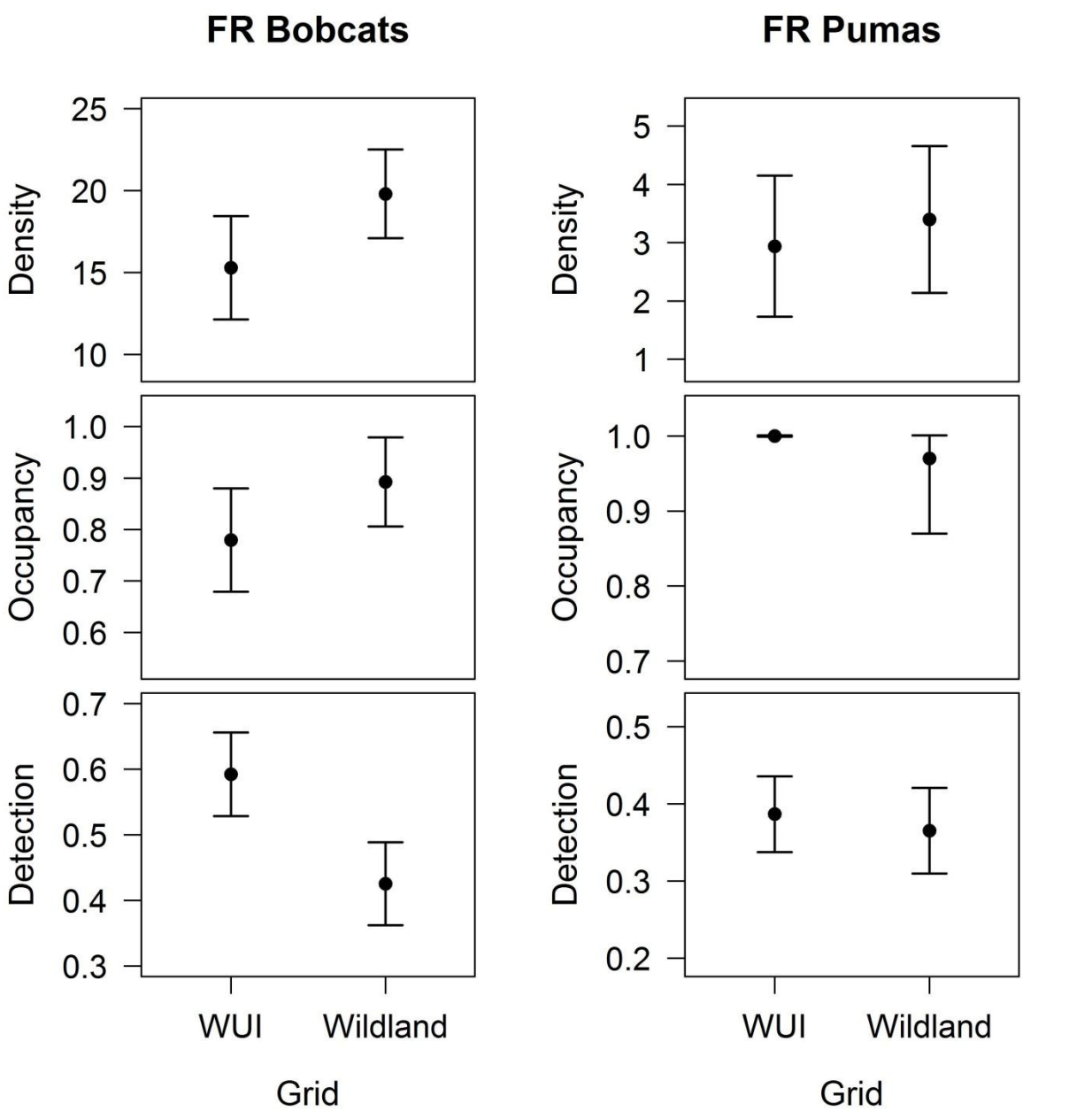


Figure 1. Locations of two study sites in Colorado, USA, which exhibited varying levels of urbanization, where bobcats and pumas were fit with GPS collars and grids of motion-activated cameras were maintained. The more rural Western Slope (WS) was characterized by an exurban development south grid and a wildland north grid during 2009 – 2010. The more urbanized Front Range (FR) study area was characterized by a wildland-urban interface (WUI) south grid and wildland north grid during 2010 – 2012.


WS Bobcats
WS Pumas
Density
Occupancy
Detection
25
20
15
4
3
2
1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
Exurban
Wildland
Grid

2a.



2b.

Figure 2. Estimates and associated standard errors for population density (# individuals per 100 km^2), site occupancy, and species detection probability of bobcats and pumas in relation to exurban and wildland grids on the Western Slope (WS) in 2009 (a) and wildland-urban interface (WUI) and wildland grids on the Front Range (FR) in 2010 (b).

LITERATURE CITED

Adler, G. H. and R. Levins. 1994. The island syndrome in rodent populations. Quarterly Review of Biology:473-490.

Alonso, R. S. 2012. The effects of urbanization and road development on carnivores in southern California. Colorado State University.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, NY.

Beier, P., S. P. D. Riley, and R. M. Sauvajot. 2010. Mountain lions (Puma concolor). Pages 141-155 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban carnivores: ecology, conflict and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soulé. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications **7**:552-563.

Bradley, C. A. and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology & Evolution **22**:95-102.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950-2000. Ecological Applications **15**:1851-1863.

Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere **1**:1-21.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition edition. Springer Verlag, New York, NY, USA.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, and M. Kinnaird. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation **4**:75-79.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Chace, J. F. and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning **74**:46-69.

Cooch, E. and G. White. 2012. Program MARK: a gentle introduction, 11th edition, <http://www.phidot.org/software/mark/docs/book/>.

Crooks, K., S. Riley, S. Gehrt, T. Gosselink, and T. Van Deelen. 2010. Community ecology of urban carnivores. Pages 185-196 *in* S. Gehrt, S. Riley, and B. Cypher, editors. Urban carnivores: ecology, conflict, and conservation. The John Hopkins University Press, Baltimore, MD, USA.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology **16**:488-502.

Crooks, K. R. and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. Journal of Mammalogy **56**:177-198.
Ellis, M. M., J. S. Ivan, and M. K. Schwartz. 2014. Spatially explicit power analyses for occupancy-based monitoring of wolverine in the US Rocky Mountains. Conservation Biology **28**:52-62.
Ferguson, A. W., N. A. Currit, and F. W. Weckerly. 2009. Isometric scaling in home-range size of male and female bobcats (Lynx rufus). Canadian Journal of Zoology **87**:1052-1060.
Freckleton, R., J. Gill, D. Noble, and A. Watkinson. 2005. Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. Journal of Animal Ecology **74**:353-364.
Fretwell, S. D. 1972. Population in a seasonal environment. Princeton University Press, Princeton, NJ, USA.
Gaston, K. J., T. M. Blackburn, J. J. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance–occupancy relationships. Journal of Applied Ecology **37**:39-59.
Gehrt, S. D., S. P. Riley, and B. L. Cypher. 2010. Urban carnivores: ecology, conflict, and conservation. John Hopkins University Press, Baltimore, MD, USA.
Germaine, S. S. and B. F. Wakeling. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation **97**:229-237.
Gittleman, J. L., S. M. Funk, D. Macdonald, and R. K. Wayne, editors. 2001. Carnivore conservation. Cambridge University Press, Canbridge, UK.
Gompper, M. E. and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia **87**:343-348.
Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald, and M. L. Johnson. 2002. Ecological and allometric determinants of home-range size for mountain lions (Puma concolor). Animal Conservation **5**:317-324.
Hadidian, J., S. Prange, R. Rosatte, S. Riley, and S. Gehrt. 2010. Raccoons (Procyon lotor). Pages 35-47 *in* S. Gehrt, S. Riley, and B. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications **15**:1893-1905.
Heilbrun, R. D., N. J. Silvy, M. E. Tewes, and M. J. Peterson. 2003. Using automatically triggered cameras to individually identify bobcats. Wildlife Society Bulletin:748-755.
Irwin, E. G. and N. E. Bockstael. 2007. The evolution of urban sprawl: evidence of spatial heterogeneity and increasing land fragmentation. Proceedings of the National Academy of Sciences **104**:20672-20677.
Karanth, K. U., J. D. Nichols, and N. S. Kumar. 2010. Estimating tiger abundance from camera trap data: field surveys and analytical issues. Pages 97-117 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Tokyo, Japan.
Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. Ecology **50**:587-607.
Kreeger, T. J., J. M. Arnemo, and J. P. Raath. 2002. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado.

Laake, J. and E. Rexstad. 2013. RMark—an alternative approach to building linear models in MARK.*in* E. G. Cooch and G. C. White, editors. Program MARK:A Gentle Introduction.
Lembeck, M. and G. I. Gould. 1979. Dynamics of harvested and unharvested bobcat populations in California. Pages 53-54 Bobcat Research Conference Proceedings: Current Research on Biology and Management of *Lynx rufus*. National Wildlife Federation Scientific Technical Series 6, Front Royal, VA.
Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. Landscape and Urban Planning **101**:99-107.
Logan, K. A. and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C.
Lukacs, P. M., K. P. Burnham, and D. R. Anderson. 2010. Model selection bias and Freedman's paradox. Annals of the Institute of Statistical Mathematics **62**:117-125.
MacKenzie, D. I. and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation **27**:461-467.
MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, CA.
MacKenzie, D. I. and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105-1114.
Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Boston, MA.
McClintock, B. T. 2012. Mark-resight models. Pages 18-11 to 18-37 *in* E. Cooch and G. White, editors. Program MARK: a gentle introduction, 11th edition, <http://www.phidot.org/software/mark/docs/book/>.
McClintock, B. T. and G. C. White. 2012. From NOREMARK to MARK: software for estimating demographic parameters using mark–resight methodology. Journal of Ornithology **152**:641-650.
McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009. Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics **65**:237-246.
McDonald, R. I., P. Kareiva, and R. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation **141**:1695-1703.
McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience **52**:883-890.
McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127**:247-260.
McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban ecosystems **11**:161-176.
Merenlender, A. M., S. E. Reed, and K. L. Heise. 2009. Exurban development influences woodland bird composition. Landscape and Urban Planning **92**:255-263.
Milinski, M. 1988. Games fish play: making decisions as a social forager. Trends in Ecology & Evolution **3**:325-330.
Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution **10**:58-62.

Nelson, A. C. and T. W. Sanchez. 2005. The effectiveness of urban containment regimes in reducing exurban sprawl. The Planning Review **41**:42-47.
Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology **26**:432-441.
Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.
O'Connell, A. F., J. D. Nichols, and U. K. Karanth. 2010. Camera traps in animal ecology: Methods and analyses. Springer Verlag, Tokyo, Japan.
Ottaviani, D., S. C. Cairns, M. Oliverio, and L. Boitani. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. Journal of Zoology **269**:317-330.
Pollock, J. F. 2006. Detecting population peclines over large areas with presence-absence, time-to-encounter, and count survey methods. Conservation Biology **20**:882-892.
Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. The Journal of Wildlife Management **67**:324-333.
R. Development Core Team 2014. R: a language and environment for statistical computing, Version 3.0.2. R Foundation for Statistical Computing. Vienna, Austria.
Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. Ecological Applications **15**:799-805.
Riley, S., E. Boydston, K. Crooks, and L. Lyren. 2010. Bobcats (Lynx rufus). Pages 121-138 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Riley, S. P., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology **17**:566-576.
Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology **15**:1733-1741.
Royle, A. and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology **84**:777-790.
Royle, J. A., J. D. Nichols, and M. Kéry. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos **110**:353-359.
Ruell, E. W., S. P. Riley, M. R. Douglas, J. P. Pollinger, and K. R. Crooks. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture-recapture sampling. Journal of Mammalogy **90**:129-135.
Ruth, T. K. and K. Murphy. 2010. Cougar-prey relationships. Pages 138-162 *in* M. Hornocker and S. Negri, editors. Cougar: ecology and conservation. University of Chicago Press, Chicago, IL.
Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, and A. Kinzig. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.
Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution **1**:103-113.

Seto, K. C., B. Güneralp, and L. R. Hutyra. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences **109**:16083-16088.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution **21**:186-191.

Soulsbury, C., P. Baker, G. Iossa, and S. Harris. 2010. Red foxes (Vulpes vulpes). Pages 63-78 *in* S. Gehrt, S. Riley, and B. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. Johns Hopkins University Press, Baltimore, Maryland.

Strayer, D. L. 1999. Statistical power of presence-absence data to detect population declines. Conservation Biology **13**:1034-1038.

Sunquist, M. and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, IL, USA.

Temple, D. and R. Gutiérrez. 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conservation Biology **27**:1087-1095.

Theobald, D. M. 2004. Placing exurban land-use change in a human modification framework. Frontiers in Ecology and the Environment **2**:139-144.

Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society **10**:1-34.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study **46**:120-139.

White, G. C. and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329-350 *in* J. Millspaugh and J. Marzluff, editors. Design and analysis of wildlife radiotelemetry studies. Academic Press, San Diego, California, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.

Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS One **8**:e60590.

Appendices Table 1. Mark-resight population size models and covariate estimates for bobcats on the Western Slope (WS), CO, exurban grid 1.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
15	α(TSOG + Weight) σ(= 0)	4	56.87	0.00	0.60	43.16	2.56	0.52	0.22	0.09	-	-	-	-
10	α(TSOG) σ(= 0)	3	58.10	1.23	0.33	49.10	2.29	0.52	-	-	-	-	-	-
6	α(TSOG) σ(.)	4	62.26	5.39	0.04	48.55	2.26	0.56	-	-	-	-	-	-
11	α(TSOG + Weight) σ(.)	5	63.16	6.29	0.03	43.16	2.56	0.52	0.22	0.09	-	-	-	-
7	α(TSOG) σ(TSOG)	5	67.09	10.22	0.00	47.09	2.06	0.60	-	-	206.70	0.00	-	-
9	α(TSOG) σ(Weight)	5	67.90	11.02	0.00	47.90	2.16	0.60	-	-	-	-	0.38	0.45
1	α(.) σ(.)	3	69.70	12.83	0.00	60.70	-	-	-	-	-	-	-	-
2	α(.) σ(TSOG)	4	71.10	14.22	0.00	57.38	-	-	-	-	6.76	27.82	-	-
12	α(TSOG + Weight) σ(TSOG)	6	71.96	15.09	0.00	43.16	2.56	0.52	0.22	0.09	7.80	3743.43	-	-
14	α(TSOG + Weight) σ(Weight)	6	71.96	15.09	0.00	43.16	2.56	0.52	0.22	0.09	-	-	0.05	505.50
4	α(.) σ(Weight)	4	72.95	16.08	0.00	59.24	-	-	-	-	-	-	0.20	0.17
16	α(Weight) σ(.)	4	74.36	17.48	0.00	60.64	-	-	0.04	0.14	-	-	-	-
8	α(TSOG) σ(TSOG + Weight)	6	75.89	19.02	0.00	47.09	2.06	0.60	-	-	93.71	0.00	93.45	0.00
3	α(.) σ(TSOG + Weight)	5	76.03	19.16	0.00	56.03	-	-	-	-	3.27	3.67	0.28	0.32
5	α(.) σ(= 0)	2	78.87	21.99	0.00	73.53	-	-	-	-	-	-	-	-
17	α(Weight) σ(TSOG)	5	78.90	22.03	0.00	58.90	-	-	-0.03	0.11	24.59	0.00	-	-
19	α(Weight) σ(Weight)	5	79.22	22.35	0.00	59.22	-	-	0.03	0.14	-	-	0.19	0.16
20	α(Weight) σ(= 0)	3	81.46	24.59	0.00	72.46	-	-	0.08	0.08	-	-	-	-
18	α(Weight) σ(TSOG + Weight)	6	84.57	27.70	0.00	55.77	-	-	-0.07	0.14	2.64	3.01	0.36	0.37
13	α(TSOG + Weight) σ(TSOG + Weight)	7	85.16	28.29	0.00	43.16	2.56	0.52	0.22	0.09	25.97	0.00	1.84	0.00
						Model Averaged	2.45	0.52	0.14	0.07	na	na	na	na
						Variable Importance Values	1.00		0.63		0.00		0.00	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 2. Mark-resight population size models and covariate estimates for bobcats on the Western Slope (WS), CO, wildland grid 2.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
5	α(.) σ(= 0)	2	55.15	0.00	0.42	49.65	-	-	-	-	-	-	-	-
10	α(TSOG) σ(= 0)	3	56.41	1.26	0.22	46.98	1.16	0.73	-	-	-	-	-	-
1	α(.) σ(.)	3	56.72	1.57	0.19	47.29	-	-	-	-	-	-	-	-
20	α(Weight) σ(= 0)	3	58.97	3.82	0.06	49.54	-	-	0.07	0.20	-	-	-	-
6	α(TSOG) σ(.)	4	60.46	5.31	0.03	45.80	1.12	0.89	-	-	-	-	-	-
2	α(.) σ(TSOG)	4	61.24	6.09	0.02	46.58	-	-	-	-	6.45	13.19	-	-
4	α(.) σ(Weight)	4	61.40	6.24	0.02	46.73	-	-	-	-	-	-	-0.31	0.40
15	α(TSOG + Weight) σ(= 0)	4	61.50	6.35	0.02	46.83	1.18	0.74	0.08	0.20	-	-	-	-
16	α(Weight) σ(.)	4	61.82	6.66	0.01	47.15	-	-	0.11	0.30	-	-	-	-
9	α(TSOG) σ(Weight)	5	67.04	11.89	0.00	45.04	1.19	0.88	-	-	-	-	-0.47	0.58
11	α(TSOG + Weight) σ(.)	5	67.66	12.51	0.00	45.66	1.13	0.90	0.10	0.27	-	-	-	-
7	α(TSOG) σ(TSOG)	5	67.78	12.63	0.00	45.78	1.21	1.17	-	-	-0.31	2.43	-	-
3	α(.) σ(TSOG + Weight)	5	67.94	12.79	0.00	45.94	-	-	-	-	37.13	30.96	-1.74	1.54
17	α(Weight) σ(TSOG)	5	68.35	13.20	0.00	46.35	-	-	0.12	0.25	7.24	17.62	-	-
19	α(Weight) σ(Weight)	5	68.63	13.48	0.00	46.63	-	-	0.10	0.30	-	-	-0.29	0.39
14	α(TSOG + Weight) σ(Weight)	6	78.00	22.85	0.00	45.00	1.19	0.89	0.06	0.29	-	-	-0.43	0.57
12	α(TSOG + Weight) σ(TSOG)	6	78.63	23.48	0.00	45.63	1.29	1.26	0.11	0.27	-0.45	2.54	-	-
18	α(Weight) σ(TSOG + Weight)	6	78.77	23.62	0.00	45.77	-	-	0.10	0.25	38.29	29.37	-1.76	1.51
8	α(TSOG) σ(TSOG + Weight)	6	78.78	23.63	0.00	45.78	1.21	1.17	-	-	-0.16	1690.68	-0.15	1690.68
13	α(TSOG + Weight) σ(TSOG + Weight)	7	96.33	41.18	0.00	45.00	1.21	1.07	0.06	0.30	-0.06	1.78	-0.43	0.57
						Model Averaged	0.32	0.41	0.01	0.07	na	na	na	na
						Variable Importance Values	0.27		0.10		0.02		0.02	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 3. Mark-resight population size models and covariate estimates for bobcats on the Western Slope (WS), CO, exurban grid 1 and wildland grid 2 combined.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
10	α(TSOG + Weight) σ(= 0)	4	100.65	0.00	0.37	90.15	2.01	0.45	0.21	0.08	-	-	-	-
11	α(TSOG) σ(.)	4	102.03	1.38	0.18	91.53	1.63	0.55	-	-	-	-	-	-
6	α(TSOG + Weight) σ(.)	5	102.93	2.28	0.12	88.93	1.85	0.52	0.18	0.10	-	-	-	-
15	α(TSOG) σ(= 0)	3	104.03	3.38	0.07	96.62	1.75	0.43	-	-	-	-	-	-
12	α(TSOG) σ(TSOG)	5	104.32	3.67	0.06	90.32	1.28	0.59	-	-	3.31	4.70	-	-
14	α(TSOG) σ(Weight)	5	104.40	3.75	0.06	90.40	1.50	0.53	-	-	-	-	0.28	0.28
2	α(.) σ(TSOG)	4	104.80	4.15	0.05	94.30	-	-	-	-	4.55	4.17	-	-
1	α(.) σ(.)	3	106.46	5.81	0.02	99.05	-	-	-	-	-	-	-	-
7	α(TSOG + Weight) σ(TSOG)	6	106.75	6.10	0.02	88.75	1.61	0.65	0.14	0.11	2.33	5.92	-	-
9	α(TSOG + Weight) σ(Weight)	6	106.81	6.16	0.02	88.81	1.76	0.58	0.16	0.12	-	-	0.14	0.41
3	α(.) σ(TSOG + Weight)	5	107.28	6.63	0.01	93.28	-	-	-	-	3.00	2.42	0.16	0.18
17	α(Weight) σ(TSOG)	5	108.19	7.54	0.01	94.19	-	-	0.04	0.10	-	-	4.08	3.36
4	α(.) σ(Weight)	4	108.28	7.63	0.01	97.78	-	-	-	-	-	-	0.17	0.16
13	α(TSOG) σ(TSOG + Weight)	6	108.32	7.67	0.01	90.32	1.28	0.59	-	-	0.21	0.00	3.10	0.00
16	α(Weight) σ(.)	4	109.26	8.61	0.00	98.76	-	-	0.07	0.12	-	-	-	-
8	α(TSOG + Weight) σ(TSOG + Weight)	7	110.40	9.75	0.00	87.79	1.47	0.58	0.11	0.11	3.23	4.94	0.44	0.72
18	α(Weight) σ(TSOG + Weight)	6	111.20	10.55	0.00	93.20	-	-	0.00	0.11	3.40	2.95	0.18	0.20
19	α(Weight) σ(Weight)	5	111.69	11.04	0.00	97.69	-	-	0.04	0.14	-	-	0.17	0.16
5	α(.) σ(= 0)	2	113.23	12.58	0.00	108.57	-	-	-	-	-	-	-	-
20	α(Weight) σ(= 0)	3	120.62	19.97	0.00	113.21	-	-	0.10	0.07	-	-	-	-
						Model Averaged	1.60	0.48	0.10	0.07	0.50	1.71	0.08	0.34
						Variable Importance Values	0.90		0.54		0.15		0.12	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 4. Mark-resight population size models and covariate estimates for pumas on the Western Slope (WS), CO, exurban grid 1.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
2	α(.) σ(= 0)	2	36.29	0.00	1.00	26.29	-	-	-	-	-	-	-	-
4	α(Weight) σ(= 0)	3	52.61	16.33	0.00	22.61	-	-	0.04	0.02	-	-	-	-
3	α(TSOG) σ(= 0)	3	55.39	19.10	0.00	25.39	-8.42	9.03	-	-	-	-	-	-
1	α(.) σ(.)	3	56.01	19.72	0.00	26.01	-	-	-	-	-	-	-	-
						Model Averaged	0.00	0.00	0.00	0.00	na	na	na	na
						Variable Importance Values	0.00		0.00		0.00		0.00	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 5. Mark-resight population size models and covariate estimates for pumas on the Western Slope (WS), CO, wildland grid 2.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
15	α(Weight) σ(= 0)	3	51.02	0.00	0.47	37.02	-	-	0.06	0.02	-	-	-	-
1	α(.) σ(.)	3	51.12	0.11	0.44	37.12	-	-	-	-	-	-	-	-
7	α(TSOG + Weight) σ(= 0)	4	54.82	3.81	0.07	26.82	2.72	0.87	0.06	0.01	-	-	-	-
5	α(.) σ(= 0)	2	59.92	8.90	0.01	52.92	-	-	-	-	-	-	-	-
4	α(.) σ(Weight)	4	60.20	9.18	0.00	32.20	-	-	-	-	-	-	0.06	0.05
11	α(TSOG) σ(= 0)	3	61.81	10.79	0.00	47.81	1.56	0.68	-	-	-	-	-	-
12	α(Weight) σ(.)	4	62.00	10.98	0.00	34.00	-	-	0.05	0.02	-	-	-	-
2	α(.) σ(TSOG)	4	62.46	11.44	0.00	34.46	-	-	-	-	4.10	3.57	-	-
8	α(TSOG) σ(.)	4	63.70	12.68	0.00	35.70	1.68	1.47	-	-	-	-	-	-
6	α(TSOG + Weight) σ(.)	5	96.82	45.81	0.00	26.82	2.72	0.87	0.06	0.01	-	-	-	-
3	α(.) σ(TSOG + Weight)	5	101.26	50.25	0.00	31.26	-	-	-	-	2.60	3.72	0.06	0.05
10	α(TSOG) σ(Weight)	5	101.27	50.26	0.00	31.27	0.77	1.05	-	-	-	-	0.08	0.07
14	α(Weight) σ(Weight)	5	101.80	50.79	0.00	31.80	-	-	0.01	0.03	-	-	0.07	0.07
13	α(Weight) σ(TSOG)	5	103.78	52.76	0.00	33.78	-	-	0.04	0.02	1.46	2.56	-	-
9	α(TSOG) σ(TSOG)	5	104.00	52.98	0.00	34.00	0.71	1.06	-	-	4.02	5.90	-	-
						Model Averaged	0.19	0.35	0.03	0.01	0.00	0.00	0.00	0.00
						Variable Importance Values	0.07		0.54		0.00		0.00	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 6. Mark-resight population size models and covariate estimates for pumas on the Western Slope (WS), CO, exurban grid 1 and wildland grid 2 combined.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
10	α(TSOG + Weight) σ(= 0)	4	60.33	0.00	0.81	44.33	2.48	0.62	0.06	0.01	-	-	-	-
1	α(.) σ(.)	3	65.37	5.04	0.07	55.37	-	-	-	-	-	-	-	-
4	α(.) σ(Weight)	4	65.76	5.43	0.05	49.76	-	-	-	-	-	-	0.06	0.05
16	α(Weight) σ(.)	4	67.63	7.29	0.02	51.63	-	-	0.05	0.02	-	-	-	-
2	α(.) σ(TSOG)	4	68.31	7.97	0.02	52.31	-	-	-	-	2.91	1.91	-	-
11	α(TSOG) σ(.)	4	69.04	8.71	0.01	53.04	2.23	1.08	-	-	-	-	-	-
6	α(TSOG + Weight) σ(.)	5	69.33	9.00	0.01	44.33	2.48	0.62	0.06	0.01	-	-	-	-
20	α(Weight) σ(= 0)	3	69.52	9.18	0.01	59.52	-	-	0.07	0.01	-	-	-	-
3	α(.) σ(TSOG + Weight)	5	74.31	13.98	0.00	49.31	-	-	-	-	1.88	2.20	0.04	0.04
14	α(TSOG) σ(Weight)	5	74.38	14.04	0.00	49.38	0.94	0.99	-	-	-	-	0.05	0.04
19	α(Weight) σ(Weight)	5	74.42	14.09	0.00	49.42	-	-	0.02	0.03	-	-	0.05	0.06
17	α(Weight) σ(TSOG)	5	75.39	15.06	0.00	50.39	-	-	0.04	0.02	1.89	1.55	-	-
12	α(TSOG) σ(TSOG)	5	76.44	16.11	0.00	51.44	3.07	0.73	-	-	2.67	1.77	-	-
7	α(TSOG + Weight) σ(TSOG)	6	83.51	23.18	0.00	43.51	2.53	0.74	0.06	0.01	-13.58	25.52	-	-
15	α(TSOG) σ(= 0)	3	83.78	23.45	0.00	73.78	2.37	0.52	-	-	-	-	-	-
9	α(TSOG + Weight) σ(Weight)	6	84.33	24.00	0.00	44.33	2.48	0.62	0.06	0.01	-	-	-0.17	0.00
18	α(Weight) σ(TSOG + Weight)	6	88.63	28.30	0.00	48.63	-	-	0.02	0.02	2.05	2.66	0.04	0.04
13	α(TSOG) σ(TSOG + Weight)	6	91.87	31.54	0.00	51.87	0.45	0.88	-	-	6.04	0.00	-1.35	0.00
5	α(.) σ(= 0)	2	98.37	38.04	0.00	92.66	-	-	-	-	-	-	-	-
8	α(TSOG + Weight) σ(TSOG + Weight)	7	112.81	52.47	0.00	42.81	2.71	0.69	0.06	0.01	-15.84	68.05	-0.12	0.26
						Model Averaged	2.07	0.58	0.05	0.01	0.05	0.28	0.00	0.01
						Variable Importance Values	0.83		0.85		0.02		0.06	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 7. Mark-resight population size models and covariate estimates for bobcats on the Front Range (FR), CO, wildland-urban interface grid 1.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
1	α(.) σ(.)	3	55.13	0.00	0.84	44.33	-	-	-	-	-	-	-	-
6	α(TSOG) σ(.)	4	60.26	5.13	0.06	42.26	2.46	1.58	-	-	-	-	-	-
16	α(Weight) σ(.)	4	61.99	6.86	0.03	43.99	-	-	-0.30	0.47	-	-	-	-
2	α(.) σ(TSOG)	4	62.24	7.11	0.02	44.24	-	-	-	-	0.26	0.84	-	-
4	α(.) σ(Weight)	4	62.29	7.16	0.02	44.29	-	-	-	-	-	-	0.05	0.23
10	α(TSOG) σ(= 0)	3	63.53	8.40	0.01	52.73	1.97	0.82	-	-	-	-	-	-
5	α(.) σ(= 0)	2	64.90	9.77	0.01	58.90	-	-	-	-	-	-	-	-
20	α(Weight) σ(= 0)	3	68.96	13.84	0.00	58.16	-	-	-0.18	0.21	-	-	-	-
15	α(TSOG + Weight) σ(= 0)	4	70.34	15.21	0.00	52.34	1.89	0.81	-0.14	0.22	-	-	-	-
9	α(TSOG) σ(Weight)	5	71.96	16.83	0.00	41.96	2.54	1.56	-	-	-	-	0.18	0.31
11	α(TSOG + Weight) σ(.)	5	72.00	16.88	0.00	42.00	2.34	1.57	-0.24	0.44	-	-	-	-
7	α(TSOG) σ(TSOG)	5	72.25	17.12	0.00	42.25	2.49	1.62	-	-	-0.12	1.38	-	-
19	α(Weight) σ(Weight)	5	73.59	18.46	0.00	43.59	-	-	-0.41	0.47	-	-	0.16	0.23
17	α(Weight) σ(TSOG)	5	73.97	18.84	0.00	43.97	-	-	-0.24	0.51	0.15	0.91	-	-
3	α(.) σ(TSOG + Weight)	5	74.17	19.04	0.00	44.17	-	-	-	-	0.36	1.09	0.07	0.29
14	α(TSOG + Weight) σ(Weight)	6	95.31	40.18	0.00	41.31	2.55	1.62	-0.34	0.43	-	-	0.28	0.28
12	α(TSOG + Weight) σ(TSOG)	6	96.00	40.87	0.00	42.00	2.38	1.60	-0.22	0.44	-0.10	1.35	-	-
8	α(TSOG) σ(TSOG + Weight)	6	96.25	41.12	0.00	42.25	2.49	1.62	-	-	0.94	433.23	-1.06	433.23
18	α(Weight) σ(TSOG + Weight)	6	97.52	42.39	0.00	43.52	-	-	-0.38	0.47	0.29	1.17	0.17	0.28
13	α(TSOG + Weight) σ(TSOG + Weight)	7	167.25	112.12	0.00	41.25	2.50	1.59	-0.33	0.43	0.30	1.72	0.30	0.40
						Model Averaged	0.19	0.47	-0.01	0.08	0.01	0.13	0.00	0.04
						Variable Importance Values	0.08		0.03		0.02		0.02	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 8. Mark-resight population size models and covariate estimates for bobcats on the Front Range (FR), CO, wildland grid 2.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
5	α(.) σ(= 0)	2	46.18	0.00	0.69	40.47	-	-	-	-	-	-	-	-
1	α(.) σ(.)	3	50.05	3.87	0.10	40.05	-	-	-	-	-	-	-	-
15	α(TSOG) σ(= 0)	3	50.07	3.89	0.10	40.07	0.47	0.74	-	-	-	-	-	-
20	α(Weight) σ(= 0)	3	50.46	4.28	0.08	40.46	-	-	0.01	0.13	-	-	-	-
4	α(.) σ(Weight)	4	55.35	9.17	0.01	39.35	-	-	-	-	-	-	-0.29	0.43
11	α(TSOG) σ(.)	4	55.73	9.54	0.01	39.73	0.48	0.84	-	-	-	-	-	-
2	α(.) σ(TSOG)	4	56.00	9.82	0.01	40.00	-	-	-	-	-0.47	2.40	-	-
16	α(Weight) σ(.)	4	56.03	9.85	0.01	40.03	-	-	0.02	0.15	-	-	-	-
10	α(TSOG + Weight) σ(= 0)	4	56.05	9.87	0.00	40.05	0.47	0.74	0.01	0.13	-	-	-	-
14	α(TSOG) σ(Weight)	5	63.51	17.33	0.00	38.51	0.77	0.84	-	-	-	-	-0.35	0.38
3	α(.) σ(TSOG + Weight)	5	63.81	17.63	0.00	38.81	-	-	-	-	-4.86	12.73	-1.48	3.95
19	α(Weight) σ(Weight)	5	63.90	17.71	0.00	38.90	-	-	0.12	0.22	-	-	-0.35	0.36
12	α(TSOG) σ(TSOG)	5	64.53	18.35	0.00	39.53	0.62	0.91	-	-	-0.94	2.18	-	-
6	α(TSOG + Weight) σ(.)	5	64.72	18.54	0.00	39.72	0.47	0.84	0.01	0.15	-	-	-	-
17	α(Weight) σ(TSOG)	5	64.94	18.76	0.00	39.94	-	-	0.04	0.17	-0.71	2.44	-	-
18	α(Weight) σ(TSOG + Weight)	6	77.36	31.18	0.00	37.36	-	-	0.22	0.24	-4.76	7.81	-1.50	2.47
9	α(TSOG + Weight) σ(Weight)	6	78.11	31.93	0.00	38.11	0.73	0.83	0.13	0.22	-	-	-0.38	0.31
7	α(TSOG + Weight) σ(TSOG)	6	79.45	33.27	0.00	39.45	0.63	0.92	0.04	0.16	-1.10	2.08	-	-
13	α(TSOG) σ(TSOG + Weight)	6	79.53	33.35	0.00	39.53	0.62	0.91	-	-	-8.89	0.00	7.94	0.00
8	α(TSOG + Weight) σ(TSOG + Weight)	7	106.43	60.25	0.00	36.43	0.96	0.89	0.19	0.24	-2.89	4.87	-0.81	1.33
						Model Averaged	0.05	0.25	0.00	0.04	0.00	0.22	0.00	0.05
						Variable Importance Values	0.11		0.09		0.01		0.01	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 9. Mark-resight population size models and covariate estimates for bobcats on the Front Range (FR), CO, wildland-urban interface grid 1 and wildland grid 2 combined.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
1	α(.) σ(.)	3	84.83	0.00	0.43	76.98	-	-	-	-	-	-	-	-
11	α(TSOG) σ(.)	4	87.00	2.18	0.15	75.67	1.04	0.90	-	-	-	-	-	-
4	α(.) σ(Weight)	4	87.16	2.34	0.13	75.83	-	-	-	-	-	-	-0.18	0.17
16	α(Weight) σ(.)	4	88.24	3.41	0.08	76.90	-	-	-0.04	0.13	-	-	-	-
2	α(.) σ(TSOG)	4	88.31	3.48	0.08	76.98	-	-	-	-	0.07	1.19	-	-
14	α(TSOG) σ(Weight)	5	89.66	4.83	0.04	74.21	1.06	0.83	-	-	-	-	-0.21	0.18
6	α(TSOG + Weight) σ(.)	5	91.04	6.21	0.02	75.59	1.04	0.90	-0.04	0.13	-	-	-	-
12	α(TSOG) σ(TSOG)	5	91.05	6.22	0.02	75.59	1.12	0.95	-	-	-0.33	1.18	-	-
19	α(Weight) σ(Weight)	5	91.22	6.39	0.02	75.77	-	-	0.04	0.15	-	-	-0.19	0.18
3	α(.) σ(TSOG + Weight)	5	91.29	6.46	0.02	75.83	-	-	-	-	-0.01	1.19	-0.18	0.17
17	α(Weight) σ(TSOG)	5	92.35	7.52	0.01	76.90	-	-	-0.04	0.13	0.11	1.22	-	-
9	α(TSOG + Weight) σ(Weight)	6	94.56	9.73	0.00	74.16	1.05	0.82	0.03	0.14	-	-	-0.22	0.18
5	α(.) σ(= 0)	2	94.98	10.15	0.00	90.12	-	-	-	-	-	-	-	-
15	α(TSOG) σ(= 0)	3	95.12	10.29	0.00	87.27	0.95	0.57	-	-	-	-	-	-
7	α(TSOG + Weight) σ(TSOG)	6	95.92	11.09	0.00	75.52	1.11	0.95	-0.04	0.13	-0.32	1.21	-	-
13	α(TSOG) σ(TSOG + Weight)	6	95.99	11.16	0.00	75.59	1.12	0.95	-	-	2.02	284.44	-2.35	284.44
18	α(Weight) σ(TSOG + Weight)	6	96.17	11.34	0.00	75.77	-	-	0.04	0.15	-0.02	1.14	-0.19	0.18
20	α(Weight) σ(= 0)	3	97.10	12.28	0.00	89.26	-	-	-0.08	0.08	-	-	-	-
10	α(TSOG + Weight) σ(= 0)	4	97.84	13.01	0.00	86.50	0.94	0.58	-0.07	0.08	-	-	-	-
8	α(TSOG + Weight) σ(TSOG + Weight)	7	100.45	15.63	0.00	74.01	1.14	0.87	0.03	0.14	-0.45	1.07	-0.22	0.17
						Model Averaged	0.24	0.44	0.00	0.05	0.00	11.46	-0.04	11.45
						Variable Importance Values	0.23		0.13		0.13		0.21	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 10. Mark-resight population size models and covariate estimates for pumas on the Front Range (FR), CO, wildland-urban interface grid 1.

							Covariates[a]									
							α						σ			
							TSOG			Weight			TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance		β	se		β	se		β	se	β	se
2	α(.) σ(= 0)	2	41.15	0.00	1.00	31.15	-	-		-	-		-	-		-	-
4	α(Weight) σ(= 0)	3	55.71	14.55	0.00	25.71	-	-			0.16	0.08	-	-		-	-
1	α(.) σ(.)	3	59.35	18.20	0.00	29.35	-	-		-	-		-	-		-	-
3	α(TSOG) σ(= 0)	3	60.39	19.24	0.00	30.39		0.80	0.92	-	-		-	-		-	-
						Model Averaged		0.00	0.00		0.00	0.00		0.00	0.00	0.00	0.00
						Variable Importance Values		0.00			0.00			0.00		0.00	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 11. Mark-resight population size models and covariate estimates for pumas on the Front Range (FR), CO, wildland grid 2.

							Covariates[a]									
							α						σ			
							TSOG			Weight			TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance		β	se		β	se		β	se	β	se
2	α(.) σ(= 0)	2	36.19	0.00	0.97	28.19	-	-		-	-		-	-		-	-
3	α(TSOG) σ(= 0)	3	44.84	8.65	0.01	26.84		0.91	0.80	-	-		-	-		-	-
4	α(Weight) σ(= 0)	3	46.19	10.00	0.01	28.19	-	-			0.00	0.01	-	-		-	-
1	α(.) σ(.)	3	46.19	10.00	0.01	28.19	-	-		-	-		-	-		-	-
						Model Averaged		0.01	0.10		0.00	0.00		0.00	0.00	0.00	0.00
						Variable Importance Values		0.01			0.01			0.00		0.00	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 12. Mark-resight population size models and covariate estimates for pumas on the Front Range (FR), CO, wildland-urban interface grid 1 and wildland grid 2 combined.

							Covariates[a]							
							α				σ			
							TSOG		Weight		TSOG		Weight	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
5	α(.) σ(= 0)	2	61.48	0.00	0.53	55.76	-	-	-	-	-	-	-	-
15	α(TSOG) σ(= 0)	3	63.62	2.15	0.18	53.62	0.86	0.60	-	-	-	-	-	-
1	α(.) σ(.)	3	64.02	2.54	0.15	54.02	-	-	-	-	-	-	-	-
20	α(Weight) σ(= 0)	3	65.74	4.26	0.06	55.74	-	-	0.00	0.01	-	-	-	-
2	α(.) σ(TSOG)	4	67.02	5.54	0.03	51.02	-	-	-	-	-3.10	1.87	-	-
11	α(TSOG) σ(.)	4	68.30	6.83	0.02	52.30	1.03	0.81	-	-	-	-	-	-
10	α(TSOG + Weight) σ(= 0)	4	69.62	8.15	0.01	53.62	0.86	0.60	0.00	0.01	-	-	-	-
4	α(.) σ(Weight)	4	69.81	8.33	0.01	53.81	-	-	-	-	-	-	-0.02	0.06
16	α(Weight) σ(.)	4	70.00	8.52	0.01	54.00	-	-	0.00	0.02	-	-	-	-
12	α(TSOG) σ(TSOG)	5	75.61	14.13	0.00	50.61	0.58	0.91	-	-	-2.72	1.92	-	-
3	α(.) σ(TSOG + Weight)	5	75.95	14.47	0.00	50.95	-	-	-	-	-2.97	1.87	-0.02	0.11
17	α(Weight) σ(TSOG)	5	76.01	14.54	0.00	51.01	-	-	0.00	0.01	-3.11	1.88	-	-
14	α(TSOG) σ(Weight)	5	77.20	15.72	0.00	52.20	1.03	0.83	-	-	-	-	-0.02	0.05
6	α(TSOG + Weight) σ(.)	5	77.30	15.83	0.00	52.30	1.03	0.82	0.00	0.02	-	-	-	-
19	α(Weight) σ(Weight)	5	78.78	17.30	0.00	53.78	-	-	0.00	0.01	-	-	-0.02	0.06
7	α(TSOG + Weight) σ(TSOG)	6	90.60	29.13	0.00	50.60	0.58	0.91	0.00	0.01	-2.73	1.93	-	-
13	α(TSOG) σ(TSOG + Weight)	6	90.61	29.13	0.00	50.61	0.58	0.91	-	-	-0.62	0.00	-2.10	0.00
18	α(Weight) σ(TSOG + Weight)	6	90.94	29.47	0.00	50.94	-	-	0.00	0.01	-2.99	1.88	-0.02	0.11
9	α(TSOG + Weight) σ(Weight)	6	92.19	30.72	0.00	52.19	1.03	0.84	0.00	0.01	-	-	-0.02	0.05
8	α(TSOG + Weight) σ(TSOG + Weight)	7	121.05	59.57	0.00	51.05	0.29	0.61	0.00	0.01	-3.08	1.07	-0.11	0.00
						Model Averaged	0.18	0.30	0.00	0.00	-0.11	0.39	0.00	0.01
						Variable Importance Values	0.21		0.08		0.03		0.01	

[a] α = alpha (intercept for mean resighting rate); σ = sigma (individual heterogeneity level); Weight = weight (kg) of animal; TSOG = time spent on grid for individual animal based on telemetry locations. See text for futher description of parameters.

[b](.) denotes intercept only model; (= 0) indicates that parameter was fixed to zero

Appendices Table 13. Occupancy models and covariate estimates for bobcats on the Western Slope (WS).

							Covariates[a]							
							Ψ				p			
							Grid		HumDev		Grid		HumDev	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
3	Ψ(.) p(Grid + HumDev)	4	273.53	0.00	0.41	264.39	-	-	-	-	-0.89	0.30	-0.37	0.17
11	Ψ(Grid) p(Grid + HumDev)	5	275.42	1.89	0.16	263.65	-22.90	0.00	-	-	-0.78	0.32	-0.38	0.17
15	Ψ(HumDev) p(Grid + HumDev)	5	276.15	2.62	0.11	264.39	-	-	1.77	933.01	-0.89	0.30	-0.37	0.17
2	Ψ(.) p(Grid)	3	276.47	2.94	0.10	65.51	-	-	-	-	-0.77	0.29	-	-
7	Ψ(Grid + HumDev) p(Grid + HumDev)	6	278.07	4.54	0.04	263.53	-29.21	0.00	3.57	822.83	-0.78	0.32	-0.38	0.17
10	Ψ(Grid) p(Grid)	4	278.48	4.95	0.03	65.04	-18.35	0.00	-	-	-0.68	0.31	-	-
4	Ψ(.) p(HumDev)	3	278.85	5.31	0.03	272.18	-	-	-	-	-	-	-0.31	0.16
14	Ψ(HumDev) p(Grid)	4	278.95	5.42	0.03	269.81	-	-	2.36	0.00	-0.77	0.29	-	-
12	Ψ(Grid) p(HumDev)	4	279.10	5.57	0.03	269.96	-16.76	0.00	-	-	-	-	-0.32	0.16
1	Ψ(.) p(.)	2	280.60	7.07	0.01	39.08	-	-	-	-	-	-	-	-
16	Ψ(HumDev) p(HumDev)	4	280.77	7.23	0.01	271.62	-	-	95.07	0.00	-	-	-0.31	0.16
9	Ψ(Grid) p(.)	3	280.96	7.43	0.01	70.00	-19.62	0.00	-	-	-	-	-	-
6	Ψ(Grid + HumDev) p(Grid)	5	281.00	7.47	0.01	269.23	-31.16	0.00	3.64	1473.96	-0.68	0.31	-	-
8	Ψ(Grid + HumDev) p(HumDev)	5	281.54	8.01	0.01	269.77	-26.00	0.00	3.50	531.82	-	-	-0.32	0.16
13	Ψ(HumDev) p(.)	3	282.47	8.94	0.00	275.81	-	-	92.03	0.00	-	-	-	-
5	Ψ(Grid + HumDev) p(.)	4	283.27	9.73	0.00	274.12	-28.72	0.00	3.94	1414.32	-	-	-	-
						Model Averaged	na	na	na	na	-0.75	0.29	-0.29	0.15
						Variable Importance Values	0.30		0.21		0.90		0.79	

[a] Ψ = occupancy (proportion of the landscape occupied by the species), p = detection probability (the probability of detecting a species given that it was present at a site); Effort = time varying survey effort covariate; Grid = covariate comparing urban (=0) and wildland (=1) grids; HumDev = kernel density human development covariate.

[b] (.) denotes intercept only model

Appendices Table 14. Occupancy models and covariate estimates for pumas on the Western Slope (WS).

							Covariates[a]							
							Ψ				p			
							Grid		HumDev		Grid		HumDev	
Model #	Model[a,b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se
4	Ψ(.) p(HumDev)	3	213.70	0.00	0.24	207.03	-	-	-	-	-	-	-0.82	0.45
13	Ψ(HumDev) p(.)	3	215.17	1.47	0.12	208.50	-	-	-0.70	0.53	-	-	-	-
3	Ψ(.) p(Grid + HumDev)	4	215.49	1.79	0.10	206.35	-	-	-	-	0.34	0.42	-0.77	0.44
1	Ψ(.) p(.)	2	215.66	1.96	0.09	33.01	-	-	-	-	-	-	-	-
12	Ψ(Grid) p(HumDev)	4	216.14	2.44	0.07	207.00	0.14	0.74	-	-	-	-	-0.82	0.45
16	Ψ(HumDev) p(HumDev)	4	216.14	2.44	0.07	207.00	-	-	-0.25	1.12	-	-	-0.73	0.64
14	Ψ(HumDev) p(Grid)	4	216.26	2.56	0.07	207.11	-	-	-0.69	0.52	0.48	0.41	-	-
2	Ψ(.) p(Grid)	3	216.52	2.82	0.06	45.79	-	-	-	-	0.50	0.41	-	-
5	Ψ(Grid + HumDev) p(.)	4	217.64	3.94	0.03	208.50	0.05	0.73	-0.69	0.53	-	-	-	-
9	Ψ(Grid) p(.)	3	217.90	4.20	0.03	47.17	0.22	0.69	-	-	-	-	-	-
15	Ψ(HumDev) p(Grid + HumDev)	5	218.04	4.34	0.03	206.28	-	-	-0.36	1.02	0.36	0.42	-0.61	0.71
11	Ψ(Grid) p(Grid + HumDev)	5	218.11	4.41	0.03	206.35	0.02	0.77	-	-	0.34	0.43	-0.77	0.44
8	Ψ(Grid + HumDev) p(HumDev)	5	218.74	5.04	0.02	206.98	0.11	0.77	-0.20	1.29	-	-	-0.75	0.67
6	Ψ(Grid + HumDev) p(Grid)	5	218.85	5.14	0.02	207.08	-0.14	0.78	-0.71	0.54	0.50	0.42	-	-
10	Ψ(Grid) p(Grid)	4	218.99	5.29	0.02	45.79	0.06	0.72	-	-	0.49	0.42	-	-
7	Ψ(Grid + HumDev) p(Grid + HumDev)	6	220.82	7.12	0.01	206.27	-0.06	0.79	-0.38	1.02	0.37	0.44	-0.60	0.72
						Model Averaged	0.02	0.35	-0.20	0.48	0.14	0.24	-0.44	0.38
						Variable Importance Values	0.22		0.36		0.32		0.57	

[a] Ψ = occupancy (proportion of the landscape occupied by the species), p = detection probability (the probability of detecting a species given that it was present at a site); Effort = time varying survey effort covariate; Grid = covariate comparing urban (=0) and wildland (=1) grids; HumDev = kernel density human development covariate.

[b] (.) denotes intercept only model

Appendices Table 15. Occupancy models and covariate estimates for bobcats on the Front Range (FR).

							Covariates[a]									
							Ψ				p					
							Grid		HumDev		Effort		Grid		HumDev	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se	β	se
4	Ψ(.) p(Effort + Grid + HumDev)	5	257.91	0.00	0.33	246.14	-	-	-	-	1.97	1.05	-0.78	0.38	-0.57	0.22
5	Ψ(.) p(Effort + HumDev)	4	259.60	1.69	0.14	250.45	-	-	-	-	1.68	1.00	-	-	-0.40	0.19
12	Ψ(Grid) p(Effort + Grid + HumDev)	6	259.71	1.80	0.13	245.16	1.09	1.28	-	-	2.05	1.06	-0.84	0.39	-0.56	0.22
16	Ψ(HumDev) p(Effort + Grid + HumDev)	6	260.67	2.76	0.08	246.12	-	-	-0.08	0.53	1.98	1.05	-0.78	0.38	-0.56	0.23
2	Ψ(.) p(Effort)	3	261.76	3.85	0.05	255.09	-	-	-	-	1.64	1.00	-	-	-	-
13	Ψ(Grid) p(Effort + HumDev)	5	261.77	3.87	0.05	250.01	0.65	1.00	-	-	1.71	1.00	-	-	-0.38	0.20
17	Ψ(HumDev) p(Effort + HumDev)	5	262.22	4.31	0.04	250.45	-	-	-0.03	0.58	1.68	1.00	-	-	-0.40	0.21
1	Ψ(.) p(.)	2	262.41	4.51	0.03	30.08	-	-	-	-	-	-	-	-	-	-
8	Ψ(Grid + HumDev) p(Effort + Grid + HumDev)	7	262.64	4.73	0.03	245.14	1.13	1.30	0.08	0.58	2.04	1.06	-0.84	0.39	-0.56	0.23
3	Ψ(.) p(Effort + Grid)	4	263.09	5.18	0.02	253.95	-	-	-	-	1.76	1.03	-0.36	0.34	-	-
10	Ψ(Grid) p(Effort)	4	263.33	5.42	0.02	254.19	0.92	1.05	-	-	1.69	1.01	-	-	-	-
14	Ψ(HumDev) p(Effort)	4	263.86	5.95	0.02	254.72	-	-	-0.24	0.38	1.65	1.01	-	-	-	-
11	Ψ(Grid) p(Effort + Grid)	5	264.34	6.43	0.01	252.58	1.28	1.36	-	-	1.87	1.04	-0.44	0.35	-	-
9	Ψ(Grid + HumDev) p(Effort + HumDev)	6	264.53	6.62	0.01	249.98	0.70	1.05	0.10	0.63	1.71	1.00	-	-	-0.39	0.21
15	Ψ(HumDev) p(Effort + Grid)	5	265.25	7.34	0.01	253.48	-	-	-0.27	0.37	1.78	1.03	-0.38	0.34	-	-
6	Ψ(Grid + HumDev) p(Effort)	5	265.88	7.97	0.01	254.11	0.83	1.12	-0.11	0.42	1.69	1.01	-	-	-	-
7	Ψ(Grid + HumDev) p(Effort + Grid)	6	267.04	9.13	0.00	252.49	1.19	1.41	-0.12	0.41	1.87	1.04	-0.45	0.35	-	-
						Model Averaged	0.27	0.64	-0.01	0.24	1.81	1.04	-0.48	0.30	-0.43	0.19
						Variable Importance Values	0.27		0.20		0.97		0.63		0.82	

[a] Ψ = occupancy (proportion of the landscape occupied by the species), p = detection probability (the probability of detecting a species given that it was present at a site); Effort = time varying survey effort covariate; Grid = covariate comparing urban (=0) and wildland (=1) grids; HumDev = kernel density human development covariate.

[b] (.) denotes intercept only model

Appendices Table 16. Occupancy models and covariate estimates for pumas on the Front Range (FR).

							Covariates[a]									
							Ψ				p					
							Grid		HumDev		Effort		Grid		HumDev	
Model #	Model[a, b]	K	AICc	ΔAICc	ω_i	Deviance	β	se	β	se	β	se	β	se	β	se
5	Ψ(.) p(Effort + HumDev)	4	263.15	0.00	0.20	254.00	-	-	-	-	1.89	1.09	-	-	-0.34	0.21
2	Ψ(.) p(Effort)	3	264.10	0.95	0.12	257.43	-	-	-	-	1.76	1.08	-	-	-	-
6	Ψ(Grid + HumDev) p(Effort)	5	264.29	1.14	0.11	252.53	-287.75	0.00	-37.17	0.00	1.82	1.08	-	-	-	-
1	Ψ(.) p(.)	2	264.99	1.85	0.08	32.66	-	-	-	-	-	-	-	-	-	-
4	Ψ(.) p(Effort + Grid + HumDev)	5	265.19	2.04	0.07	253.42	-	-	-	-	1.91	1.10	-0.23	0.30	-0.36	0.22
9	Ψ(Grid + HumDev) p(Effort + HumDev)	6	265.44	2.29	0.06	250.89	-457.63	1080.76	-78.27	29.04	1.90	1.08	-	-	-0.22	0.19
13	Ψ(Grid) p(Effort + HumDev)	5	265.46	2.31	0.06	253.69	-15.25	0.00	-	-	1.90	1.09	-	-	-0.33	0.22
17	Ψ(HumDev) p(Effort + HumDev)	5	265.61	2.46	0.06	253.84	-	-	154.17	0.00	1.91	1.09	-	-	-0.35	0.22
10	Ψ(Grid) p(Effort)	4	265.94	2.79	0.05	256.80	-15.56	0.00	-	-	1.78	1.08	-	-	-	-
3	Ψ(.) p(Effort + Grid)	4	266.38	3.23	0.04	257.24	-	-	-	-	1.77	1.08	-0.13	0.30	-	-
14	Ψ(HumDev) p(Effort)	4	266.53	3.39	0.04	257.39	-	-	-0.30	0.98	1.77	1.08	-	-	-	-
7	Ψ(Grid + HumDev) p(Effort + Grid)	6	267.05	3.90	0.03	252.50	-240.24	3494.39	-32.73	112.26	1.82	1.08	-0.05	0.30	-	-
16	Ψ(HumDev) p(Effort + Grid + HumDev)	6	267.84	4.69	0.02	253.30	-	-	151.44	0.00	1.93	1.10	-0.23	0.31	-0.37	0.22
12	Ψ(Grid) p(Effort + Grid + HumDev)	6	267.91	4.76	0.02	253.37	-15.22	0.00	-	-	1.92	1.10	-0.19	0.34	-0.35	0.22
8	Ψ(Grid + HumDev) p(Effort + Grid + HumDev)	7	268.17	5.02	0.02	250.67	-304.05	2793.06	-55.93	75.08	1.91	1.09	-0.15	0.31	-0.25	0.20
11	Ψ(Grid) p(Effort + Grid)	5	268.56	5.41	0.01	256.79	-14.95	0.00	-	-	1.78	1.09	-0.03	0.33	-	-
15	Ψ(HumDev) p(Effort + Grid)	5	269.00	5.85	0.01	257.23	-	-	-0.28	1.62	1.77	1.09	-0.13	0.31	-	-
						Model Averaged	na	na	na	na	1.70	1.07	-0.04	0.14	-0.17	0.15
						Variable Importance Values	0.36		0.34		0.92		0.22		0.51	

[a] Ψ = occupancy (proportion of the landscape occupied by the species), p = detection probability (the probability of detecting a species given that it was present at a site); Effort = time varying survey effort covariate; Grid = covariate comparing urban (=0) and wildland (=1) grids; HumDev = kernel density human development covariate.

[b] (.) denotes intercept only model

INTERSPECIFIC INTERACTIONS BETWEEN WILD FELIDS ACROSS A GRADIENT OF URBANIZATION [2]

OVERVIEW

In response to current and projected global impacts of urbanization, understanding the effects of human activities on competitive interactions of animals is critical due to the far-reaching effects to ecological communities and processes. We evaluated interspecific interactions between medium- and large-sized carnivores across a gradient of urbanization and multiple scales. Specifically, we investigated spatial and temporal interactions of bobcats and pumas by evaluating circadian activity patterns, broad-scale seasonal interactions, and fine-scale daily interactions in wildland-urban interface (WUI), exurban and rural residential development, and wildland habitats. As predicted, urbanization altered interspecific interactions between wild felids and appeared to increase the opportunity for carnivores to interact. Bobcats did not avoid pumas across broad spatial and temporal scales; however, bobcats responded behaviorally to the presence of pumas at finer scales, but patterns varied across levels of urbanization. In wildland habitat, bobcats avoided using areas for short temporal periods after a puma visited an area. In contrast, bobcats did not avoid areas that pumas recently visited in landscapes influenced by urbanization (exurban and WUI habitat). In addition, overlap in circadian activity patterns between bobcats and pumas increased in exurban habitat compared to wildland habitat. We explore three hypotheses to explain our results that consider activity patterns, landscape configuration, and animal scent marking. Ultimately, urbanization can lead to increased

[2] Jesse S. Lewis, Larissa L. Bailey, Sue VandeWoude, Kevin R. Crooks

opportunities for interspecific competition with potential far-reaching impacts to felid populations and the ecological community.

INTRODUCTION

Species interactions have long been recognized as a driving factor in shaping ecological communities and influencing the spatial and temporal distribution of animals (Darwin 1859, Schoener 1974, Carothers and Jaksić 1984). Gause (1934) demonstrated that two species with the same ecological requirements, or niches, could not occupy the same area (i.e., the competitive exclusion principle; Hardin 1960). However, species with seemingly similar ecological requirements can co-exist by exploiting different habitat features (e.g., Gause 1934, MacArthur 1958). In addition, two species with apparently different niches can have potentially strong interactions that influence the behavior, demography, and distribution of the subordinate species (Palomares and Caro 1999). Landscape change resulting from anthropogenic factors, such as urbanization, can alter species interactions and ecological communities in human-modified landscapes, which can have rippling effects throughout the ecosystem (Crooks and Soulé 1999, Faeth et al. 2005); however, this area of research has been relatively understudied until recently (Magle et al. 2012). Given the expansive current human footprint globally (Leu et al. 2008, Schneider et al. 2009, Nickerson et al. 2011) and projected rates of additional extensive landscape change resulting from human development (Theobald 2005, Seto et al. 2011), additional research on interspecific competition (i.e., between species) should focus on understanding how anthropogenic factors (particularly urbanization) influence species interactions and the resulting ecological implications (Magle et al. 2012). Studies comparing competition across a gradient of urbanization can further our understanding for how

anthropogenic factors alter species interactions (McDonnell and Pickett 1990, McDonnell and Hahs 2008).

Urbanization currently covers hundreds of millions of acres globally (Schneider et al. 2009, Nickerson et al. 2011) and is projected to expand by hundreds of millions of acres within the next few decades (Cohen 2003, Theobald 2005, Theobald and Romme 2007, Seto et al. 2011). Different forms of urban development, however, can result in varying landscape pattern and impacts on animals. For example, urban (<0.25 acres per residence) and suburban (0.25 – 1.68 acres per residence) residential development (Theobald 2005) can create relatively impermeable barriers to animal movement that can potentially increase population densities through altered movement patterns (Riley et al. 2006) and increased available forage (Fedriani et al. 2001, Hadidian et al. 2010) or decrease population size for species that are sensitive to urban impacts (McKinney 2008). The juxtaposition of residential development with wildland habitat (i.e., primarily natural habitat without human development) creates a wildland-urban interface (WUI), which is often characterized by a linear boundary that can significantly alter ecological processes and populations (Radeloff et al. 2005). Exurban (1.68 – 40 acres per residence) and rural (> 40 acres per residence) residential development (Theobald 2005), which is characterized by low density urban development often immersed within natural habitat, might not create barriers and can be permeable to animal movement; human disturbance from these forms of development can pervade the landscape over much broader spatial extents and alter animal behavior and population characteristics (Hansen et al. 2005, Lewis et al. 2014c). By influencing animal behavior and demography, all forms of urbanization can potentially alter interactions between species. However, despite the pervasiveness of urbanization and the associated impacts

to ecological communities, relatively little is known about how varying levels of urbanization affect interspecific competition for most animals.

Interspecific competition is broadly categorized as either exploitation (resource) or interference (contest) (Birch 1957, Schoener 1983). Exploitation competition occurs when two species indirectly compete by using the same resource (e.g., food). Interference competition involves direct (or the potential for direct) interactions, such as fighting, killing, or maintaining a territory (Schoener 1983, Carothers and Jaksić 1984). Ultimately, competition can result in spatial and temporal niche partitioning between species, which can occur across fine to broad scales. For example, sympatric species might segregate spatially across daily or seasonal periods or completely avoid areas used by competitors (Albrecht and Gotelli 2001, Kronfeld-Schor and Dayan 2003).

Competitive interactions can be particularly strong among sympatric carnivores (Rosenzweig 1966, Palomares and Caro 1999, Creel et al. 2001, Caro and Stoner 2003) and larger species can have substantial competitive effects on smaller subordinate species through asymmetrical competition (Schoener 1983, Persson 1985). Various sized carnivores often compete when one species steals or scavenges the food of another species (i.e., kleptoparasitism; Koehler and Hornocker 1991, Gorman et al. 1998, Merkle et al. 2009), which, although potentially rewarding energetically, can be especially risky when subordinate carnivores scavenge on the prey carcasses of larger species. Intra-guild predation (i.e., interspecific killing of species that are potential competitors) can be a powerful expression of interspecific competition that shapes ecological communities and animal behavior (Polis et al. 1989, Palomares and Caro 1999). Ultimately, interspecific competition can lead to subordinate species

using “competition refuges” to avoid dominant species and reduce interspecific competition spatially and temporally (Durant 1998, Berger and Gese 2007).

Two wild felids with similar geographic ranges and activity patterns across much of western North America, the bobcat (*Lynx rufus*) and puma (i.e., mountain lion, cougar, panther; *Puma concolor*), have high potential for spatial and temporal interactions (Koehler and Hornocker 1991, Sunquist and Sunquist 2002, Hass 2009). Bobcats will scavenge on the carcasses of puma prey, thus increasing the opportunity for interspecific interactions, and pumas will kill bobcats (Koehler and Hornocker 1991). In addition, the behavior, movement patterns, and population characteristics of both felids are impacted by human development and disturbance (George and Crooks 2006, Riley et al. 2006, Beier et al. 2010, Riley et al. 2010, Tracey et al. 2013, Wilmers et al. 2013), but to varying degrees (Crooks 2002), which can potentially influence interspecific competition. For example, anthropogenic barriers, such as roadways and urban development, can restrict felid movement patterns (Tracey et al. 2013) and increase space use overlap (Riley et al. 2006) and thus influence competitive interactions between these species (Crooks et al. 2010). Urban development can also influence disease transmission; in California, pumas acquired the bobcat strain of Feline Immunodeficiency Virus (FIV), presumably through increased interspecific interactions and encounter rates related to urbanization (Franklin et al. 2007). No studies, however, have explicitly evaluated interspecific interactions between bobcats and pumas or how varying levels of urbanization, including urban, exurban, and rural development (e.g., across a gradient of urbanization; Theobald 2004, Theobald and Romme 2007, McDonnell and Hahs 2008), influence their interactions. Such evaluations would provide important information about altered competitive interactions,

potential for novel modes of disease transmission, and intra-guild killing between animals across urbanizing landscapes.

We evaluated interspecific interactions between bobcats and pumas across a gradient of urbanization and multiple scales. Specifically, we investigated spatial and temporal interactions of bobcats and pumas by evaluating circadian activity patterns, broad-scale seasonal interactions (where "seasonal" refers to the entire sampling period across multiple months), and fine-scale daily interactions in wildland urban-interface (WUI), exurban, rural, and wildland habitat. Interspecific interactions were evaluated using conditional two-species (Richmond et al. 2010) and single-season (MacKenzie et al. 2006) occupancy modeling. Overall, we predicted high overlap in circadian activity patterns between bobcats and pumas and greater overlap of activity patterns in landscapes impacted by urbanization compared to wildland areas. If bobcats use "competition refuges" in space or time, we expected that bobcats would avoid pumas spatially and temporally at both fine and broad scales and hypothesized that interactions might increase in areas associated with urbanization. Further, if bobcats avoid high use areas of pumas, we expected a negative relationship between the number of puma observations at a site and detection probability of bobcats.

STUDY AREA

We conducted our research across two study sites in Colorado, USA that exhibited varying degrees of urbanization and human influence. In 2009, we worked on the Western Slope (WS) of Colorado on the Uncompahgre Plateau near the towns of Montrose and Ridgway (Figure 1). Common vegetation included pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), gambel oak

(*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). We divided the WS study site into two sampling grids. The southern grid 1 sampled exurban and rural residential development on Log Hill Mesa (population = 1,041; US Census Bureau 2010); residential parcel sizes were distributed, from most to least numerous, across 5 acre, 2 acre, 1 acre, ≥ 5 acre, and ≥ 40 acre properties. Within areas of exurban development, travel corridors of natural habitat and open space property, often with associated recreation trails, were present. The northern grid 2 sampled primarily undeveloped, wildland habitat, although some small areas of low density human residences and hunting camps occurred on or near the grid.

In 2010, we worked on the more urbanized Front Range (FR) of Colorado (Figure 1). Common vegetation included ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), juniper, aspen, and mountain mahogany (*Cercocarpus montanus*). A network of open space properties with recreational trails occurred across the study area. Similar to the WS, we divided the FR study area into two sampling grids. The southern grid 1 occurred adjacent to the wildland-urban interface associated with the city of Boulder (population = 97,385, US Census Bureau 2010) and was characterized by open-space properties with some human residences on or near the grid. The northern grid 2 occurred across undeveloped public properties, although a small number of rural human residences occurred on private property inholdings. See Lewis et al. (2014c) for an expanded description of the study area.

METHODS

Sampling Grids and Camera Surveys

Each study area (WS and FR) contained 40 motion-activated cameras divided between 2 camera grid arrays spaced approximately 6 km apart (Figure 1). Each grid was 80 km^2,

consisting of 20 4-km^2 grid cells (both grids in each study area sampled a total of 160 km^2). Within each grid cell, we placed one motion-activated camera at a site that we believed maximized the opportunity to photograph bobcats and pumas. Cameras were placed along game trails, people trails, and secondary dirt roads where felid sign (primarily scats, scrapes, and marking sites) was observed or in areas that appeared to be likely travel routes. Our sampling was passive in that we did not use attractants (i.e., sight, sound, scent) to lure animals to the camera location. We used Cuddeback (Non Typical, Inc., Green Bay, WI, USA) Capture motion-activated cameras (with a 30 second delay) with a white-flash to obtain color photographs during the day and at night, except at one site along a high-use human recreation trail on the FR where we switched to using a Cuddeback Attack Infra-Red camera to reduce vandalism. Cameras operated on the WS from 21 August to 13 December 2009 and on the FR from 1 October 2010 to 31 December 2010.

We considered photographs of bobcats and pumas taken at a camera site to be independent if images were obtained >1 hour apart. If 2 adult felids were photographed <1 hour apart and could be differentiated based on natural or artificial (i.e., telemetry collars and eartags; for details see Lewis et al. 2014c) markings, these photographs were also counted as independent animals. Kittens and dependent offspring (individuals typically of small body size and often accompanied by their mother in photographs) were not considered independent animals and were excluded from analyses. Inference from motion-activated cameras is in relation to the movement behavior of animals when traveling past sampling locations.

Circadian Activity Patterns

We compared overlap in activity patterns between bobcats and pumas across sampling grids. To estimate activity patterns of felids using circular kernel density statistics, we used the

R (R Development Core Team 2014) package Overlap (Meredith and Ridout 2013) and followed their recommendations for bandwidth selection, estimators for quantifying overlap, and 10,000 bootstrap simulations to estimate 95% confidence intervals (Ridout and Linkie 2009, Meredith and Ridout 2013). Activity throughout the day was defined as crepuscular (morning and evening), diurnal (day), and nocturnal (night).

Occupancy Modeling

We used occupancy modeling (MacKenzie et al. 2006) to evaluate interactions between bobcats and pumas across broad (seasonal) and fine (daily) scales, described below. Occupancy probability (Ψ) estimates the proportion of the landscape used by the species and detection probability (p) estimates the probability of detecting a species given that it used a site, which can evaluate the behavioral response in relation to landscape characteristics. A site refers to a camera location. All occupancy analyses were conducted in program Presence (Hines 2006).

Broad Scale: Seasonal

To evaluate species interactions on the seasonal scale (5 sampling occasions that were each 22 days long on the WS and 18 days long the FR), we used conditional two-species occupancy models (Richmond et al. 2010) where pumas were the dominant species (species A) and bobcats were the subordinate species (species B). These models consider eight parameters related to occupancy and detection probabilities; we focused on five of these parameters to evaluate the model comparisons present by Richmond et al. (2010) including Ψ^{BA} (probability of occupancy for bobcats, given pumas are present), Ψ^{Ba} (probability of occupancy of bobcats, given pumas are absent), p^{B} (probability of detection for bobcats, given pumas are absent), r^{BA} (probability of detection for bobcats, given both species are present and pumas are detected during the same sampling occasion), and r^{Ba} (probability of detection for bobcats, given both

species are present and pumas are not detected during the same sampling occasion). To evaluate if the occupancy of the subordinate species depends on the presence of the dominant species, we compared the relative performance of models where: (1) the probability of bobcat use is different on sites that are used or not used by puma (Ψ^{BA} and Ψ^{Ba} estimated separately) or (2) the probability of bobcat use of a site is independent of puma use ($\Psi^{BA} = \Psi^{Ba}$) (Richmond et al. 2010). To evaluate if bobcat detection probability was influenced by puma use, we compared the relative performance of models where detection was independent of puma use (unconditional model where $p^{B} = r^{BA} = r^{Ba}$; i.e., pumas did not alter bobcat detection probability) and models where bobcat detection was different at sites used by pumas (p^{B} is estimated separately from $r^{B.}$, where $r^{B.} = (r^{BA} = r^{Ba})$; i.e., pumas altered bobcat detection probability).

Previous research indicated that landscape covariates did not sufficiently explain occupancy of bobcats and pumas in our study, likely due to relatively high estimates of occupancy for felids and little variation in estimated use; however, detection probabilities of each species were influenced by two covariates, one that measured human influenced at each camera site (termed *human development*) and another that applied to each of the sampling grids (termed *grid*) (Lewis et al. 2014c). The covariate *human development* measured the amount of human influence (Lewis et al. 2011) associated with each camera location and was created by digitizing each human occurrence point (HOP; residence or structure) in the study areas using ArcMap10 geographic information system (GIS) software (ESRI, Redlands, CA, USA) from color orthophotos. Using Arc Toolbox in ArcMap10, we fit a Gaussian kernel over each HOP, where the density, or influence, was greatest directly at the point of interest and decreased out to a specified radius of a circle (see Lewis et al. 2014c). In GIS, each camera location was intersected with the cumulative kernel density of human development across each radius. The

covariate *grid* designated camera sites located in either exurban and wildland grids (on the WS) or wildland-urban interface and wildland grids (on the FR). We considered these two covariates when evaluating detection probability parameters in the conditional two-species interaction models. In addition, Lewis et al. (2014c) concluded that sampling effort (a time varying covariate accounting for the number of days that a camera operated for each sampling occasion) influenced detection probability on the FR, but not the WS; therefore, the covariate *effort* was included for all detection parameters on the FR in broad-scale occupancy analyses. For each broad-scale model set, we compared 20 models that evaluated how pumas affected bobcat occupancy and how pumas, *human development*, and *grid* affected bobcat detection probability.

Fine Scale: Daily

To evaluate species interactions on a daily scale, we used single-species occupancy models (MacKenzie et al. 2002, MacKenzie et al. 2006) to estimate detection probability (behavioral response) of bobcats in relation to covariates. For fine-scale models, each day represented a sampling occasion (t = 113 on the WS and t = 92 on the FR) and a species was recorded as detected if at least one photograph was documented between 12:00 (i.e., noon) of consecutive days; this definition of a day was used because of the crepuscular and nocturnal activity patterns of bobcats and pumas. To evaluate whether pumas influenced bobcat detection on a fine scale, we created multiple covariates that characterized puma detection at each site for each day *i* (i.e, if a puma was detected (1) or not (0)). First, we created a time-specific covariate (*P1*) that recorded whether a puma was detected at a site within the 24 hour period (i.e., t_i for site j = 1). We then created three additional covariates (*P2*, *P3*, *P4*) which represented lag effects of 1 to 3 days. For example, *P3* represents a covariate that would evaluate whether detection probability of bobcats was different (lower) for 3 days starting with the day a puma was detected

plus the next 2 days (i.e., *P3* covariate would be $t_i = 1$, $t_{i+1} = 1$, $t_{i+2} = 1$, when a puma was detected on day *i* at a site). Because pumas scent mark through scats, urinations, and scent glands along trails and at marking sites (Logan and Sweanor 2001), it was hypothesized that bobcats could detect the presence of pumas for up to three additional days once a puma traveled through an area; this number of days was based on the experience of researchers who use trained dogs to track pumas using the scent of animals (K. Logan personal communication). Because we predicted that competitive interactions between bobcats and pumas would be influenced by urbanization, we included interactions between the covariates *grid* and *P1*, *P2*, *P3*, and *P4*. Based on the positive relationship between local abundance and photographic rates (Carbone et al. 2001, Rovero and Marshall 2009) or detection probability (Royle and Nichols 2003), we expected a negative relationship between bobcat detection probability and the number of puma photographs recorded at a site during the study because the frequency of bobcat use may decline at sites that are often visited by pumas. We therefore included a site covariate summarizing the total number of puma photographs for each camera location (i.e., *puma count*). Similar to the broad-scale occupancy modeling, we also evaluated the influence of the *human development* and *grid* covariates on daily bobcat detection probability (Lewis et al. 2014c). Similar for broad-scale analyses, as explained above, we did not include covariates on Ψ because previous research found no variation in bobcat occupancy as estimates of occupancy were near 1 (Lewis et al. 2014c). For each fine-scale model set, we compared 21 models that evaluated how *human development*, *grid*, *puma pount*, puma lag effects (*P1 – P4*), and the interactions between *grid* and puma lag effects influenced bobcat detection probability.

RESULTS

We documented a photograph of a felid at each of our camera sites across both study areas and both species were well represented across sampling grids (Table 1).

Circadian Activity Patterns

As expected, both species were mostly active during crepuscular and nocturnal time periods, with bobcats active more during diurnal time periods than pumas, particularly on the FR (Figure 2). Puma activity peaked during the evening crepuscular and nocturnal periods, particularly on the WS wildland and both FR grids, while bobcat activity tended to be peak during the morning crepuscular and nocturnal periods (Figure 2). Overlap of activity patterns between bobcats and pumas was greater on the exurban grid compared to the wildland grid on the WS (Table 2; Figure 2a) and similar between WUI and wildland grids on the FR (Table 2; Figure 2b).

Occupancy

Broad Scale: Seasonal

At the seasonal scale, pumas did not appear to exclude bobcats from sites or impact their detection. For both the WS and FR, models that indicated there was no difference in occupancy or detection probability for bobcats in relation to puma presence were always better supported than models where bobcat occupancy and/or detection varied based on puma presence at a site (Tables 3 and 4). Consistent with Lewis et al. (2014c), *human development* and *grid* covariates improved model performance in both study areas (Tables 3 and 4).

Fine Scale: Daily

At the daily scale, puma detection explained temporal and spatial variation in bobcat detection probability in all study areas. Temporally, pumas appeared to affect the detection

probability of bobcats for relatively short periods of time (i.e., up to a few days); however, results varied across landscapes experiencing different levels of urbanization. On the WS and FR, all the top models contained bobcat detection probability structures that included an interaction between the detection of pumas (*P1 – P4* covariate) and sampling grids (Grid covariate) (Table 5 and 6). The best model for the WS data suggested an interaction between *grid* and the lag effect of pumas on bobcat detection, which lasted up to 3 days (Table 5). On the wildland grid, daily detection probability of bobcats remained at zero for three days after puma detection, and then increased towards levels observed when pumas were not detected at a site (Figure 3a). Thus, WS bobcats were less likely to be detected on a short temporal scale after pumas visited a site on the wildland grid; however this pattern was not observed on the exurban grid (Figure 4a), indicating that bobcats did not avoid pumas on short temporal scales in this type of urbanized habitat. On the FR, the most supported model indicated that bobcat detection probability was lower on the wildland grid when pumas were detected, but only up to 2 days after a puma visited a site (Table 6). Bobcat detection probability remained at 0 for two days, then increased at 3 and 4 days after a puma visit to a site (Figure 3b). However, detection probability of bobcats was similar on the FR wildland-urban interface grid when pumas were present and absent (Figure 4b), again suggesting that bobcats did not avoid pumas on fine scales in landscapes influenced by urbanization.

Spatially, pumas also influenced bobcat detection probability. Based on the top models, *puma count* demonstrated a negative relationship with bobcat detection probability on the WS ($\beta = -0.08$; se = 0.04) and FR ($\beta = -0.11$; se = 0.05); therefore, as the number of puma photos at a site increased the probability of detecting bobcats decreased (Figure 5). The number of puma photos recorded at a site ranged from 0 - 8 on the WS and 0 - 6 on the FR. Consistent with

Lewis et al. (2014c), on both the WS and FR, the covariate *human development* improved model performance and demonstrated a negative relationship with bobcat detection probability (see Lewis et al. (2014c) for a summary of results for the *human development* covariate).

DISCUSSION

Consistent with our predictions, urbanization altered interspecific interactions between wild felids and appeared to increase the opportunity for carnivores to interact. Our results demonstrate that large carnivores do not exclude subordinate carnivores across broad spatial and temporal scales; however, subordinate carnivores respond behaviorally to the presence of dominant animals at finer scales. As predicted, such avoidance patterns varied across levels of urbanization. Assuming that a lack of detection is due to avoidance of areas, in wildland habitat, bobcats avoided using areas for short temporal periods (i.e., 2 – 3 days) once a puma visited an area, but then used these sites with similar probability after approximately 4 days compared to sites where pumas were not recently detected. Bobcats likely detected the presence of pumas through markings and scent along trails and responded by altering their behavior to avoid direct interactions with a superior competitor. In contrast to wildland habitat, in landscapes influenced by urbanization (exurban and WUI habitat) bobcats did not avoid areas that pumas recently visited. In addition, in habitat characterized by low-density residential development, overlap in circadian activity patterns between bobcats and pumas increased compared to wildland habitat. Thus, urbanization can potentially lead to increased opportunities for interspecific competition with potential far-reaching impacts to felid populations and the ecological community.

Population densities of animals might increase in urbanized habitat due to greater landscape heterogeneity and food (Chace and Walsh 2006), restricted dispersal due to

anthropogenic barriers (Riley et al. 2006), or ecological release from competitors (Crooks and Soulé 1999), which can increase opportunities for interspecific interactions (Crooks et al. 2010). Our results indicated that the opportunity for interactions between felids increased in habitat influenced by urban development. This pattern, however, did not appear to be related to increased population densities of felids. In our study areas, population densities for both bobcats and pumas in exurban habitat were lower compared to wildland habitat and densities were similar between WUI and wildland habitat (Lewis et al. 2014c). We thus consider three additional hypotheses for how interspecific interactions could increase in areas influenced by urbanization.

First, animals may shape their circadian activity patterns in response to interspecific competition and are thus able to reduce the opportunity of interference competition with competitors by being active during different times of the day (Carothers and Jaksić 1984). However, if human disturbance alters wildlife activity patterns then animals might exhibit greater overlap in circadian activity and thus increase the potential for direct interactions (Hypothesis 1: increased overlap in activity patterns). For example, if animals avoid human disturbance during the day and find temporal refuge from human activities at night (e.g., George and Crooks 2006), then animals might be active during restricted temporal periods and experience greater overlap in activity patterns, which can potentially lead to intensified interactions. On the WS, anthropogenic disturbance likely altered circadian activity patterns of felids in exurban habitat, where animals were more active at night to avoid human disturbance during the day, leading to greater temporal overlap. On the FR, although we did not observe greater overlap in activity patterns between felids on WUI and wildland grids, it is possible that human disturbance emanating from urban areas could alter activity patterns of animals in other

systems, such as in smaller patches of habitat surrounded by an urban matrix, or at finer spatial scales along the wildland-urban interface. Further, human recreation, which can alter activity patterns in animals (George and Crooks 2006, Lewis and Crooks 2014), occurred across the FR and might have influenced activity of felids similarly between grids.

Second, by altering landscape pattern or increasing landscape fragmentation, human activities can potentially funnel animal movements into more restrictive areas of natural habitat, thus decreasing movement options across the landscape (Hypothesis 2: funneling animal movements). With fewer options for movement, animals are thus more likely to use similar areas and increase the opportunity for interactions. In addition, carnivores often use human recreation trails and dirt roads as travel routes, which can influence animal movement behavior (Karanth et al. 2010). If animals are more likely to use well-defined trails created by humans as travel routes, as is often the case with wild felids, animal movements, and thus potential interactions, might be more concentrated in these areas as well. On the WS and FR, animals were likely funneled into using more restrictive areas of natural habitat because they avoided using areas of human development and disturbance (Lewis et al. 2014c). On the WS, animals used natural habitat that was intermixed with low-density residential development and on the FR, a relatively impermeable urban matrix and the availability of well-defined recreation trails possibly funneled animal movement and increased the potential for interactions.

Third, human activities can potentially affect the scent marking of animals. Scent marking through scats, urinations, and scent glands is an important and widespread form of communication among animals (Ralls 1971, Wyatt 2014), especially within carnivore communities (Gorman and Trowbridge 1989, Logan and Sweanor 2001, Sunquist and Sunquist 2002). In our study, results of fine-scale interactions in wildland habitat indicate that subordinate

carnivores detect and avoid dominant carnivores via scent. Scent marking often occurs in prominent locations along trails to advertise the presence of animals, which can either be territorial (e.g., warning other animals of an individual's presence) or as an advertisement (e.g., providing information about the mating status of animals) (Wyatt 2014). Human activities, however, can destroy or mask such scent marking signals and thus disrupt communication among animals or lead animals to increase scent marking activities (Hypothesis 3: scent marking disturbance). For example, along trails used by humans, this can occur through recreationists trampling and destroying animal scent marks or domestic dogs ingesting carnivore scats (coprophagy; Soave and Brand 1991, Boze 2010) or urinating or defecating at marking sites (Bekoff 2001). The introduction of novel scents and markings from domestic dogs can also increase the use of trails by some wildlife to investigate and refresh marking sites (Lenth et al. 2008). Thus, due to scent marking disturbance, animals might be less aware of each other's presence or more active on human trails, leading to increased interspecific interactions. On the FR, high levels of human recreation on trails associated with the WUI (Vaske et al. 2009) might have disturbed carnivore markings and scent and disrupted the ability of animals to detect conspecifics through scent communication or altered marking behavior.

Additional factors could influence interspecific interactions that either we did not evaluate or could be more pronounced in other ecological systems. For example, urbanization can influence the population densities of a variety of competitors, which can alter ecological communities and competitive interactions (Crooks and Soulé 1999, Faeth et al. 2005, Crooks et al. 2010). Estimates of population density were not available for other potential competitors in our study, such as red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*); however, population densities for these species

can increase in urban-associated areas (Beckmann and Berger 2003, Gehrt et al. 2010), which could possibly influence space-use patterns and interactions among felids. Prey populations, such as small mammals and ungulates, also can potentially be influenced by urbanization (Bolger et al. 1997, Polfus and Krausman 2012, Riem et al. 2012), although it is unknown to what degree prey influenced interspecific interactions in our system. In addition, seasonal and annual variation in landscape pattern and populations of competitors and prey can alter the strength of competitive interactions through time (Wiens 1977, Schoener 1982).

In addition, in our study, as the number of puma visits increased at a site, the probability of detecting bobcats decreased, suggesting that bobcats less frequently used areas with high visitation rates by pumas. If the number of puma visits to a site was exceptionally high (indicating a strong preference for an area), then bobcat detection probability could approach 0. In our study, puma visits to a site were relatively low; but in other systems, it would be predicted that areas with high puma use could exclude bobcats. For example, other research indicates that high-use areas by dominant carnivores can influence the frequency of use by subordinate competitors, potentially leading to exclusion of the subordinate species from such areas (e.g., Durant 1998, Creel et al. 2001).

Our study provides insight into how urbanization influences interspecific interactions, with implications for the conservation and management of animal populations in developed landscapes. Our results suggest that the conversion of wildland habitat to urbanization will likely alter interactions among species and potentially affect animal populations and community structure. For example, we observed greater opportunities for encounters between bobcats and pumas in urbanized environments, which could lead to higher rates of interspecific contact and intraguild predation events and subsequently increased transmission rates of pathogens in urban

areas (Franklin et al. 2007). Further, by potentially funneling animal movements into more restrictive travel corridors, there could be increased opportunities for incidences with people and domestic animals in such areas. Ultimately, multiple mechanisms, as proposed above, can alter competition in urbanized habitat and such mechanisms might vary depending upon the form and intensity of urbanization. Such considerations can be incorporated into land-use planning to minimize impacts to wildlife communities and reduce potential interactions with people. Our findings suggest that by managing for wildland habitat and reducing human disturbance in such areas, animals will likely be better able to maintain spatial and temporal separation to reduce the potential of competitive interactions.

Table 1. Summary of photographs for felids in exurban and wildland habitat on the Western Slope (WS) and in wildland-urban interface (WUI) and wildland habitat on the Front Range (FR) of Colorado, 2009 – 2010.

Study Area[1]	Species	Grid Area	# Sites[2]	# Photos
WS	Bobcat	Exurban	20	112
WS	Bobcat	Wildland	18	73
WS	Bobcat	Total	38	185
WS	Puma	Exurban	11	39
WS	Puma	Wildland	12	41
WS	Puma	Total	23	80
FR	Bobcat	WUI	15	81
FR	Bobcat	Wildland	17	69
FR	Bobcat	Total	32	150
FR	Puma	WUI	19	50
FR	Puma	Wildland	17	46
FR	Puma	Total	36	96

[1] Sampling occurred for 113 days on the WS and 92 days on the FR

[2] The number of camera locations (sites) where the species was detected at least once. There were 20 sites on each individual grid

Table 2. Estimated overlap of activity patterns (and associated 95% confidence intervals) between bobcats and pumas in exurban and wildland habitat on the Western Slope (WS) and in wildland-urban interface (WUI) and wildland habitat on the Front Range (FR) of Colorado, 2009 – 2010.

Western Slope		Front Range	
Exurban	Wildland	WUI	Wildland
0.93 (0.86 - 0.97)	0.77 (0.62 - 0.89)	0.87 (0.77 - 0.94)	0.86 (0.76 - 0.94)

Table 3. Model selection results for broad-scale 2-species occupancy models evaluating seasonal interactions between bobcats and pumas on the Western Slope, Colorado, 2009. Parameters included Ψ^{A} (probability of occupancy for pumas), Ψ^{BA} (probability of occupancy for bobcats, given pumas are present), Ψ^{Ba} (probability of occupancy of bobcats, given pumas are absent), p^{A} (probability of detection for pumas, given bobcats are absent), r^{A} (probability of detection for pumas, given both species are present), p^{B} (probability of detection for bobcats, given pumas are absent), r^{BA} (probability of detection for bobcats, given both species are present and pumas are detected), and r^{Ba} (probability of detection for bobcats, given both species are present and pumas are not detected). Covariates included: G (sampling grid area) and HD (influence of human development at a kernel density radius of 200m).

Model [1]	K	AIC_c	ΔAICc	ω	log($\mathcal{L}$)
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (G + HD))	7	480.67	0.00	0.45	466.67
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (G + HD))	8	481.66	0.99	0.27	465.66
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (G))	6	484.37	3.70	0.07	472.37
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (HD))	6	484.49	3.82	0.07	472.49
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (HD))	7	484.77	4.10	0.06	470.77
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$ (G))	7	485.59	4.92	0.04	471.59
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$)	5	487.10	6.43	0.02	477.10
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, ($p^{B} = r^{BA} = r^{Ba}$)	6	487.53	6.86	0.01	475.53
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, p^{B}, ($r^{BA} = r^{Ba}$)	6	489.10	8.43	0.01	477.10
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, p^{B}, ($r^{BA} = r^{Ba}$)	7	489.51	8.84	0.01	475.51
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, p^{B}(G), ($r^{BA} = r^{Ba}$ (G))	9	489.54	8.87	0.01	475.54
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}, r^{A}, p^{B}, r^{BA}, r^{Ba}	7	490.94	10.27	0.00	476.94
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(HD), r^{A}(HD), p^{B}(HD), r^{BA}(HD), r^{Ba}(HD)	12	491.05	10.38	0.00	467.05
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}, r^{A}, p^{B}, r^{BA}, r^{Ba}	8	491.31	10.64	0.00	475.31
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(HD), r^{A}(HD), p^{B}(HD), r^{BA}(HD), r^{Ba}(HD)	13	491.50	10.83	0.00	465.50
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(G + HD), r^{A}(G + HD), p^{B}(G + HD), r^{BA}(G + HD), r^{Ba}(G + HD)	17	492.62	11.95	0.00	458.62
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(G), r^{A}(G), p^{B}(G), r^{BA}(G), r^{Ba}(G)	12	492.73	12.06	0.00	468.73
Ψ^{A}, Ψ^{BA},Ψ^{Ba}, p^{A}(G), r^{A}(G), p^{B}(G), ($r^{BA} = r^{Ba}$ (G))	12	492.75	12.08	0.00	468.75
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(G + HD), r^{A}(G + HD), p^{B}(G + HD), r^{BA}(G + HD), r^{Ba}(G + HD)	18	493.20	12.53	0.00	457.20
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(G), r^{A}(G), p^{B}(G) ,r^{BA}(G), r^{Ba}(G)	13	495.72	15.05	0.00	469.72

[1] To evaluate if the occupancy of bobcats depends on the presence of pumas we compared conditional occupancy models (Ψ^{BA} and Ψ^{Ba} estimated separately) to unconditional models ($\Psi^{BA} = \Psi^{Ba}$). To evaluate if the detection of bobcats was influenced by the presence of pumas we compared conditional detection models (p^{B} is estimated separately from r^{BA} and r^{Ba}, assuming $r^{BA} = r^{Ba}$) to unconditional models ($p^{B} = r^{BA} = r^{Ba}$) (Richmond et al. 2010).

Table 4. Model selection results for broad-scale 2-species occupancy models evaluating seasonal interactions between bobcats and pumas on the Front Range, Colorado, 2010. Parameters included Ψ^{A} (probability of occupancy for pumas), Ψ^{BA} (probability of occupancy for bobcats, given pumas are present), Ψ^{Ba} (probability of occupancy of bobcats, given pumas are absent), p^{A} (probability of detection for pumas, given bobcats are absent), r^{A} (probability of detection for pumas, given both species are present), p^{B} (probability of detection for bobcats, given pumas are absent), r^{BA} (probability of detection for bobcats, given both species are present and pumas are detected), and r^{Ba} (probability of detection for bobcats, given both species are present and pumas are not detected). Covariates included: G (sampling grid area), HD (influence of human development at a kernel density radius of 1300m), and E (Sampling Effort).

Model [1]	K	AIC_c	ΔAIC_c	ω	log(ℒ)
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (G + HD + E))	10	508.60	0.00	0.48	488.60
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (G + HD + E))	11	510.60	2.00	0.18	488.60
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (HD + E))	9	511.28	2.68	0.13	493.28
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (HD + E))	10	513.20	4.60	0.05	493.20
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (E))	8	513.38	4.78	0.04	497.38
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (G + E))	9	514.00	5.40	0.03	496.00
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(G + HD + E), r^{A}(G + HD + E), p^{B}(G + HD + E), r^{BA}(G + HD + E), r^{Ba}(G + HD + E)	22	514.47	5.87	0.03	470.47
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (E))	9	515.36	6.76	0.02	497.36
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), ($p^{B} = r^{BA} = r^{Ba}$ (G + E))	10	516.00	7.40	0.01	496.00
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), p^{B}(E), ($r^{BA} = r^{Ba}$ (E))	10	516.25	7.65	0.01	496.25
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(G + HD + E), r^{A}(G + HD + E), p^{B}(G + HD + E), r^{BA}(G + HD + E), r^{Ba}(G + HD + E)	23	516.47	7.87	0.01	470.47
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), p^{B}(G + E), ($r^{BA} = r^{Ba}$ (G + E))	13	517.29	8.69	0.01	491.29
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), p^{B}(E), ($r^{BA} = r^{Ba}$ (E))	11	518.24	9.64	0.00	496.24
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(HD + E), r^{A}(HD + E), p^{B}(HD + E), r^{BA}(HD + E), r^{Ba}(HD + E)	17	518.72	10.12	0.00	484.72
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(E), r^{A}(E), p^{B}(E), r^{BA}(E), r^{Ba}(E)	12	519.78	11.18	0.00	495.78
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(G + E), r^{A}(G + E), p^{B}(G + E), ($r^{BA} = r^{Ba}$ (G + E))	15	520.51	11.91	0.00	490.51
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(HD + E), r^{A}(HD + E), p^{B}(HD + E), r^{BA}(HD + E), r^{Ba}(HD + E)	18	520.70	12.10	0.00	484.70
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(E), r^{A}(E), p^{B}(E), r^{BA}(E), r^{Ba}(E)	13	521.85	13.25	0.00	495.85
Ψ^{A}, ($\Psi^{BA} = \Psi^{Ba}$), p^{A}(G + E), r^{A}(G + E), p^{B}(G + E), r^{BA}(G + E), r^{Ba}(G + E)	17	522.25	13.65	0.00	488.25
Ψ^{A}, Ψ^{BA}, Ψ^{Ba}, p^{A}(G + E), r^{A}(G + E), p^{B}(G + E), r^{BA}(G + E), r^{Ba}(G + E)	18	525.03	16.43	0.00	489.03

[1] To evaluate if the occupancy of bobcats depends on the presence of pumas we compared conditional occupancy models (Ψ^{BA} and Ψ^{Ba} estimated separately) to unconditional models ($\Psi^{BA} = \Psi^{Ba}$). To evaluate if the detection of bobcats was influenced by the presence of pumas we compared conditional detection models (p^{B} is estimated separately from r^{BA} and r^{Ba}, assuming $r^{BA} = r^{Ba}$) to unconditional models ($p^{B} = r^{BA} = r^{Ba}$) (Richmond et al. 2010).

Table 5. Model selection results for fine-scale single-species single-season occupancy models for bobcats evaluating daily interactions with pumas on the Western Slope, Colorado, 2009. Parameters included Ψ (occupancy; probability of use for bobcats) and p (detection probability for bobcats). Covariates included PumaCount (total number of independent puma photos recorded at a camera site), HD (influence of human development at a kernel density radius of 200m), G (sampling grid area), P1 (same day detection of puma, no additional lag effect), P2 (day of puma detection plus 1 additional day of lag effect), P3 (day of puma detection plus 2 additional days of lag effect), P4 (day of puma detection plus 3 additional days of lag effect), G*P (interaction term between sampling grid area and the structure of lag detection of pumas).

Model [1]	K	AIC_c	ΔAIC_c	ω	log(ℒ)
Ψ(.), p(PumaCount + HD + G + P3 + G*P3)	7	1426.06	0.00	0.52	1412.06
Ψ(.), p(PumaCount + HD + G + P2 + G*P2)	7	1426.98	0.92	0.33	1412.98
Ψ(.), p(PumaCount + HD + G + P4 + G*P4)	7	1430.27	4.21	0.06	1416.27
Ψ(.), p(G + P3 + G*P3)	5	1432.36	6.30	0.02	1422.36
Ψ(.), p(PumaCount + HD + G + P1 + G*P1)	7	1433.21	7.15	0.01	1419.21
Ψ(.), p(PumaCount + HD)	4	1433.32	7.26	0.01	1425.32
Ψ(.), p(G + P2 + G*P2)	5	1433.84	7.78	0.01	1423.84
Ψ(.), p(PumaCount + HD + P2)	5	1434.61	8.55	0.01	1424.61
Ψ(.), p(PumaCount + HD + P4)	5	1434.68	8.62	0.01	1424.68
Ψ(.), p(PumaCount + HD + P1)	5	1435.26	9.20	0.01	1425.26
Ψ(.), p(PumaCount + HD + P3)	5	1435.28	9.22	0.01	1425.28
Ψ(.), p(HD)	3	1435.60	9.54	0.00	1429.60
Ψ(.), p(G + P4 + G*P4)	5	1437.08	11.02	0.00	1427.08
Ψ(.), p(PumaCount)	3	1438.72	12.66	0.00	1432.72
Ψ(.), p(.)	2	1439.11	13.05	0.00	1435.11
Ψ(.), p(G)	3	1439.55	13.49	0.00	1433.55
Ψ(.), p(G + P1 + G*P1)	5	1439.79	13.73	0.00	1429.79
Ψ(.), p(P2)	3	1440.90	14.84	0.00	1434.90
Ψ(.), p(P4)	3	1441.03	14.97	0.00	1435.03
Ψ(.), p(P3)	3	1441.06	15.00	0.00	1435.06
Ψ(.), p(P1)	3	1441.11	15.05	0.00	1435.11

Table 6. Model selection results for fine-scale single-species single-season occupancy models for bobcats evaluating daily interactions with pumas on the Front Range, Colorado, 2010. Parameters included Ψ (occupancy; probability of use for bobcats) and p (detection probability for bobcats). Covariates included PumaCount (total number of independent puma photos recorded at a camera site), HD (influence of human development at a kernel density radius of 1300m), G (sampling grid area), P1 (same day detection of puma, no additional lag effect), P2 (day of puma detection plus 1 additional day of lag effect), P3 (day of puma detection plus 2 additional days of lag effect), P4 (day of puma detection plus 3 additional days of lag effect), G*P (interaction term between sampling grid area and the structure of lag detection of pumas).

Model [1]	K	AIC_c	ΔAIC_c	ω	log(L)
Ψ(.), p(PumaCount + HD + G + P2 + G*P2)	7	1176.81	0.00	0.45	1162.81
Ψ(.), p(PumaCount + HD + G + P3 + G*P3)	7	1179.01	2.20	0.15	1165.01
Ψ(.), p(PumaCount + HD + G + P1 + G*P1)	7	1179.15	2.34	0.14	1165.15
Ψ(.), p(G + P2 + G*P2)	5	1181.16	4.35	0.05	1171.16
Ψ(.), p(PumaCount + HD)	4	1182.27	5.46	0.03	1174.27
Ψ(.), p(PumaCount + HD + G + P4 + G*P4)	7	1182.89	6.08	0.02	1168.89
Ψ(.), p(PumaCount + HD + P2)	5	1183.18	6.37	0.02	1173.18
Ψ(.), p(G + P3 + G*P3)	5	1183.31	6.50	0.02	1173.31
Ψ(.), p(PumaCount + HD + P3)	5	1183.37	6.56	0.02	1173.37
Ψ(.), p(PumaCount)	3	1183.91	7.10	0.01	1177.91
Ψ(.), p(G + P1 + G*P1)	5	1184.01	7.20	0.01	1174.01
Ψ(.), p(HD)	3	1184.03	7.22	0.01	1178.03
Ψ(.), p(.)	2	1184.20	7.39	0.01	1180.2
Ψ(.), p(PumaCount + HD + P4)	5	1184.21	7.40	0.01	1174.21
Ψ(.), p(PumaCount + HD + P1)	5	1184.27	7.46	0.01	1174.27
Ψ(.), p(P2)	3	1184.62	7.81	0.01	1178.62
Ψ(.), p(P3)	3	1184.76	7.95	0.01	1178.76
Ψ(.), p(G)	3	1185.46	8.65	0.01	1179.46
Ψ(.), p(P4)	3	1185.91	9.10	0.00	1179.91
Ψ(.), p(P1)	3	1186.16	9.35	0.00	1180.16
Ψ(.), p(G + P4 + G*P4)	5	1187.54	10.73	0.00	1177.54

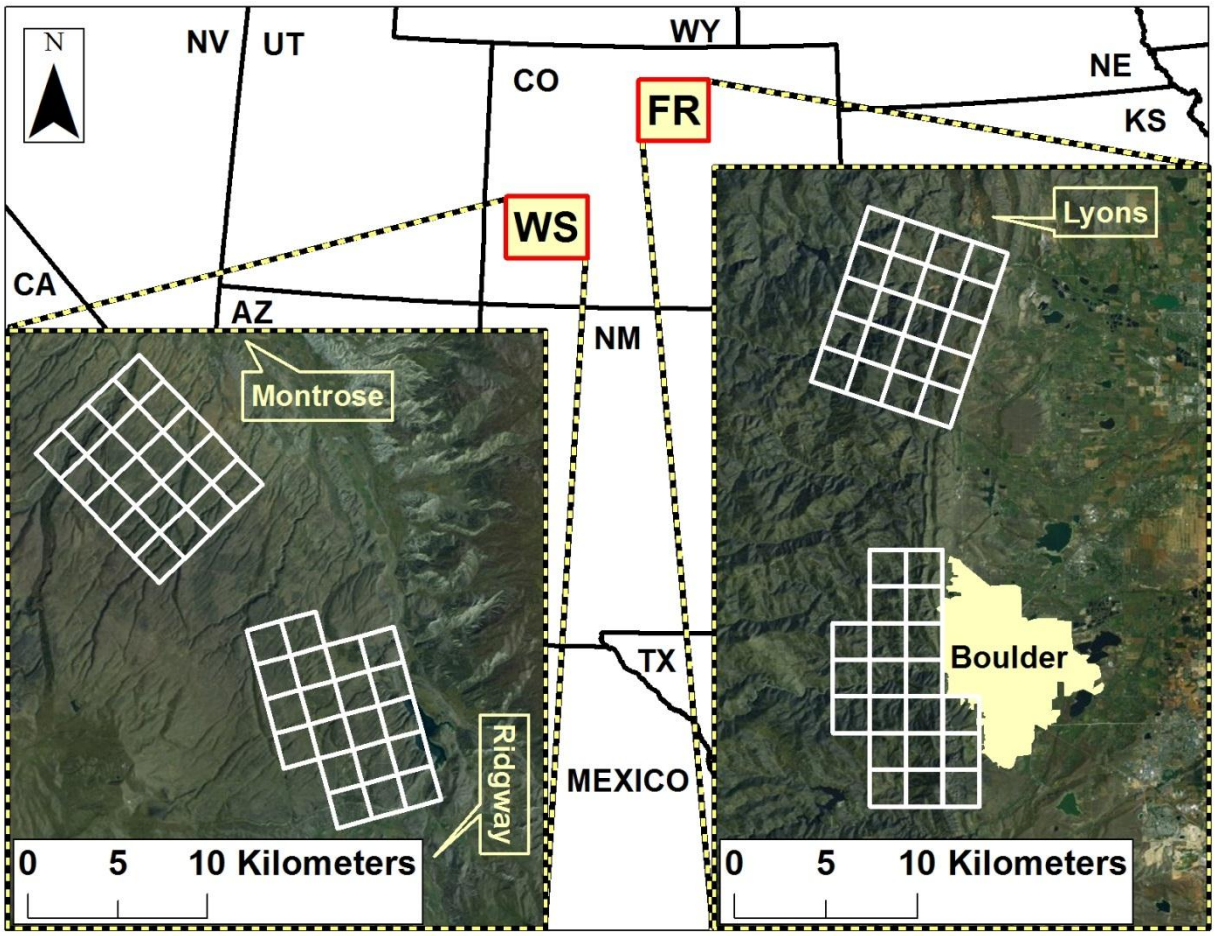


Figure 1. Motion-activated cameras were maintained across two study sites in Colorado, USA, exhibiting varying levels of urbanization. The more rural Western Slope (WS) was characterized by an exurban development south grid and a wildland north grid during 2009. The more urbanized Front Range (FR) study area was characterized by a wildland-urban interface south grid and wildland north grid during 2010.

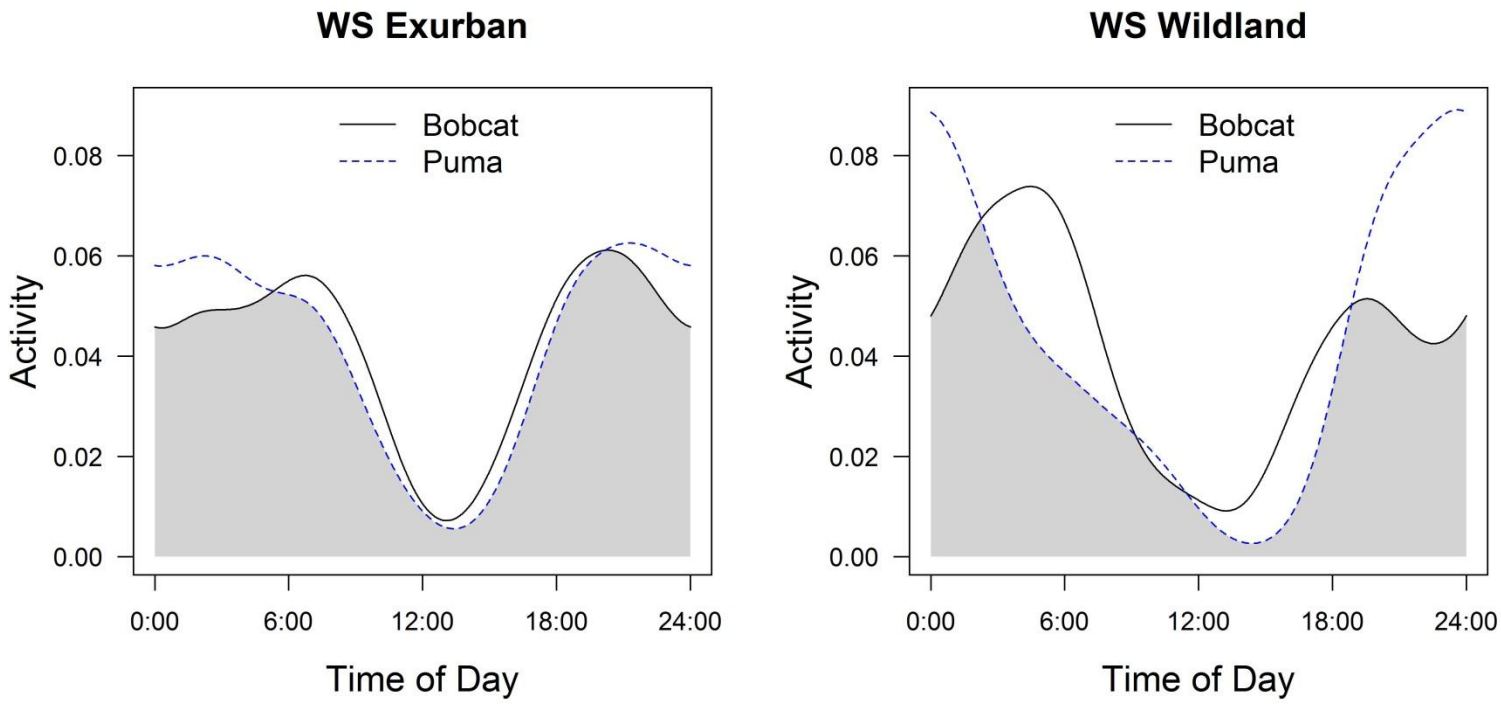


Figure 2a. WS exurban and wildland habitat activity pattern overlap

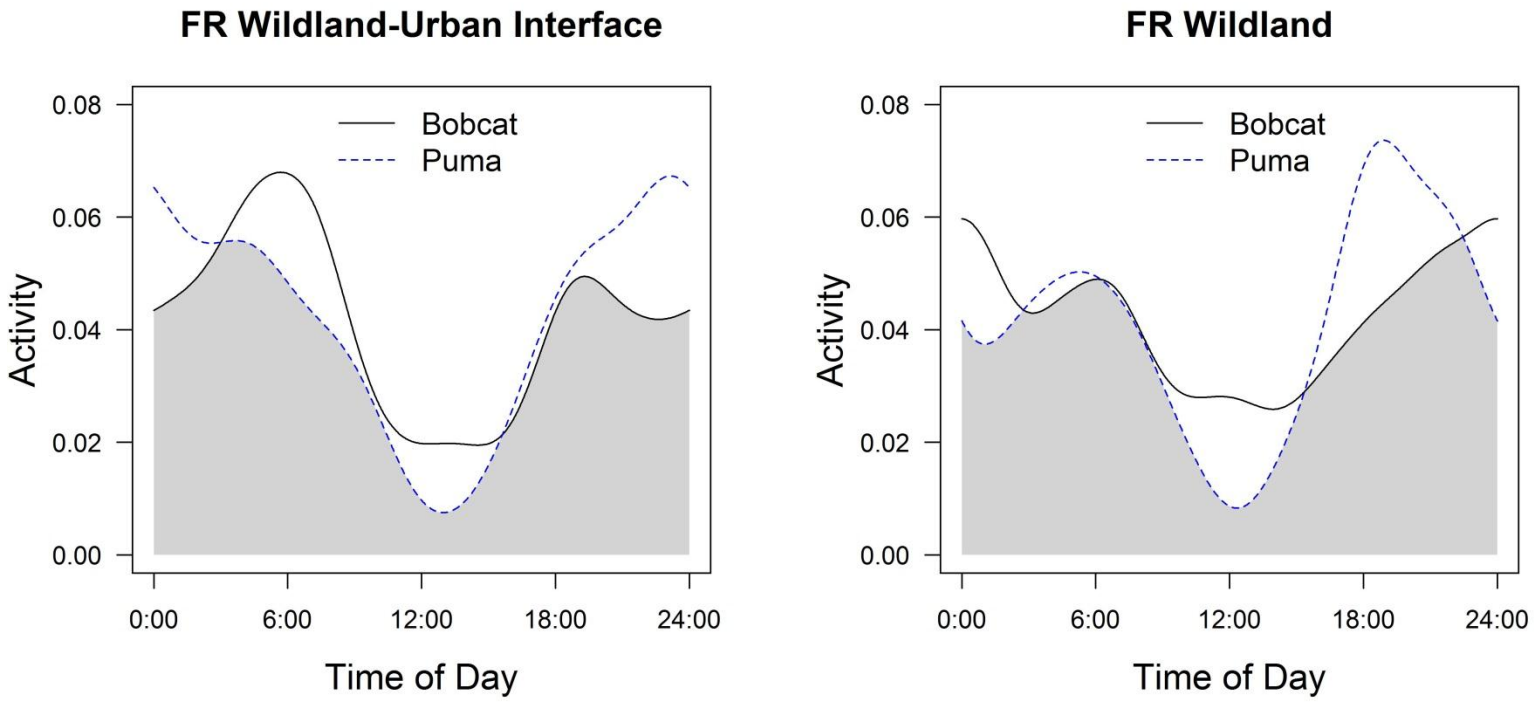


Figure 2b. FR wildland-urban interface and wildland habitat activity pattern overlap

Figure 2. Overlap in activity patterns between bobcats and pumas was greater in exurban habitat compared to wildland habitat on the Western Slope (WS) during 2009 (a) and similar between wildland-urban interface (WUI) and wildland habitat on the Front Range (FR) during 2010 (b). Kernel density is represented along the y-axis and the 24 hour circadian daily cycle occurs along the x-axis.

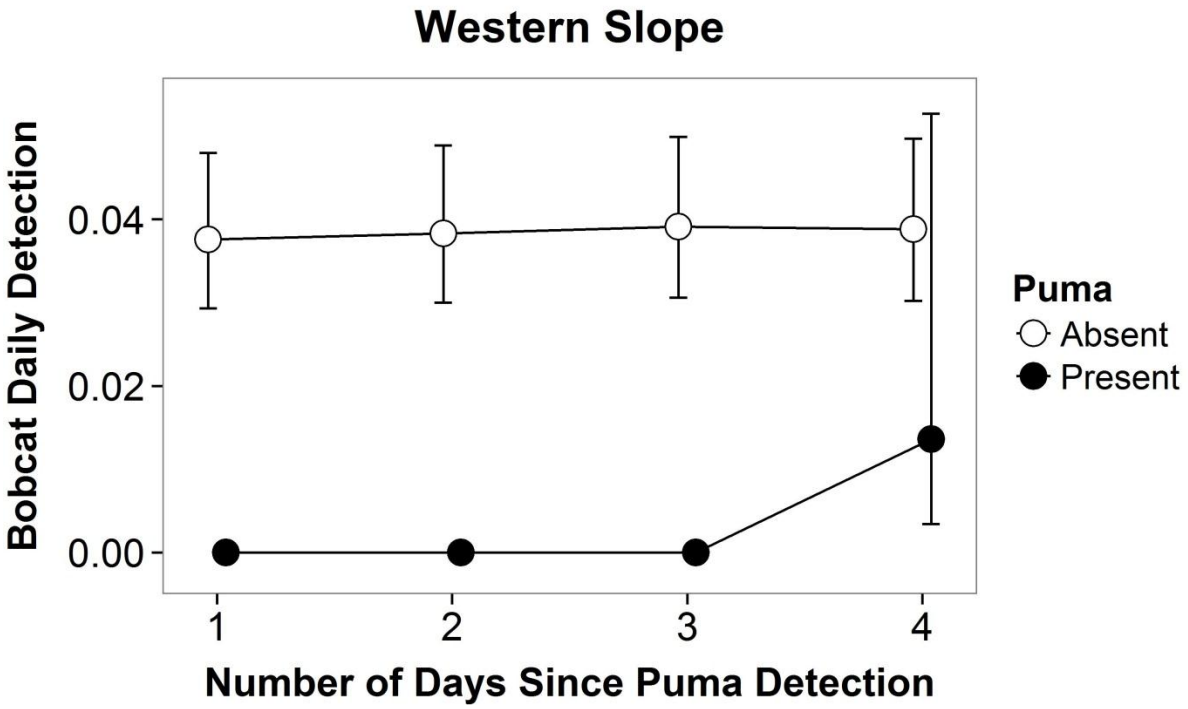


Figure 3a. Western Slope

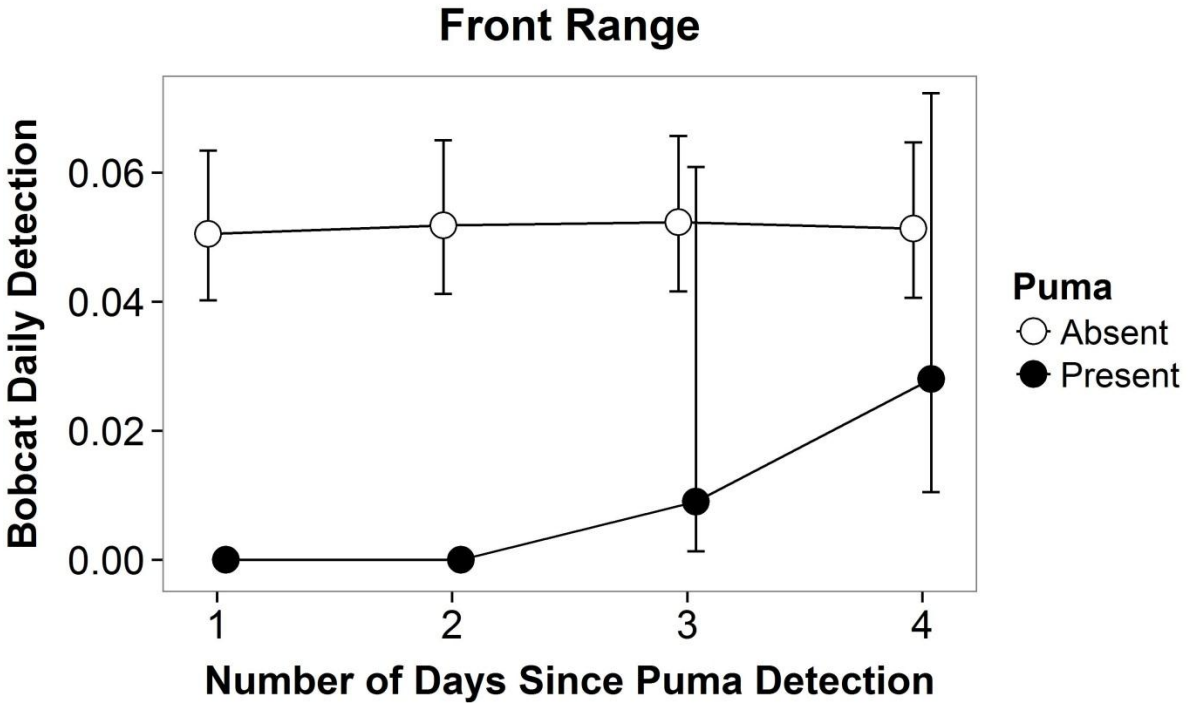


Figure 3b. Front Range

Figure 3. Bobcat daily detection probability estimates (with associated 95% confidence intervals) were lower for 2 – 3 days after a puma visited a site in wildland habitat on the Western Slope (a) and Front Range (b) of Colorado. Bobcat detection probability was evaluated in relation to 1 – 4 day lag periods of puma detection at a site considering the interaction between Grid (urbanized or wildland) and each lag effect of puma detection (P1 to P4) on bobcat detection probability. See Methods for more details).

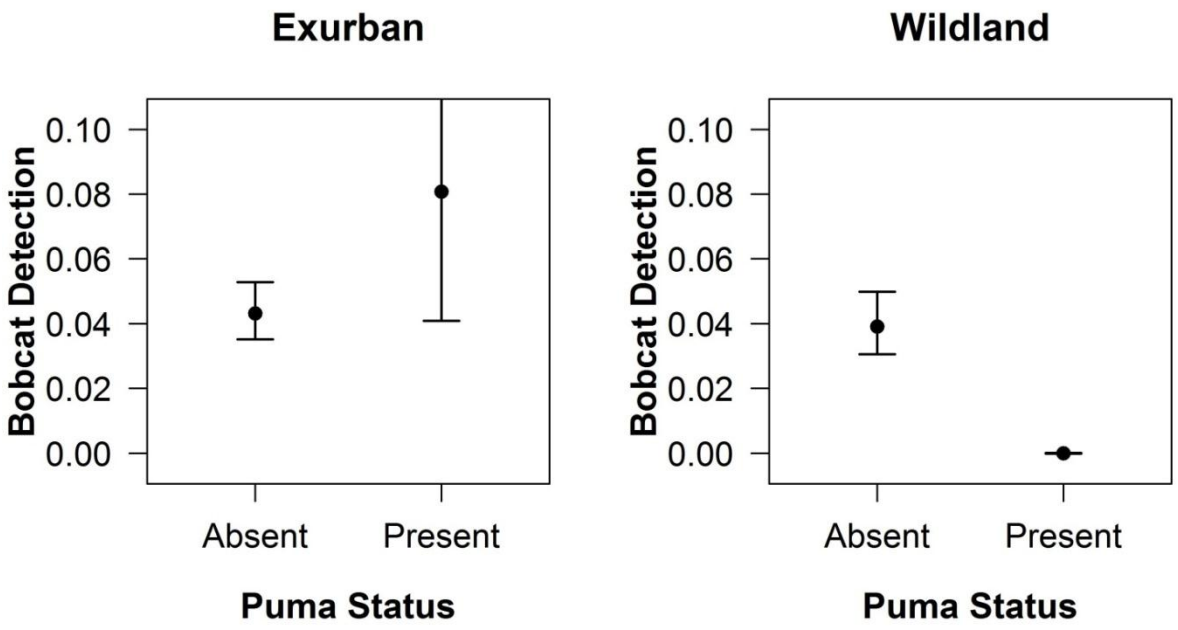


Figure 4a. WS daily bobcat detection probability

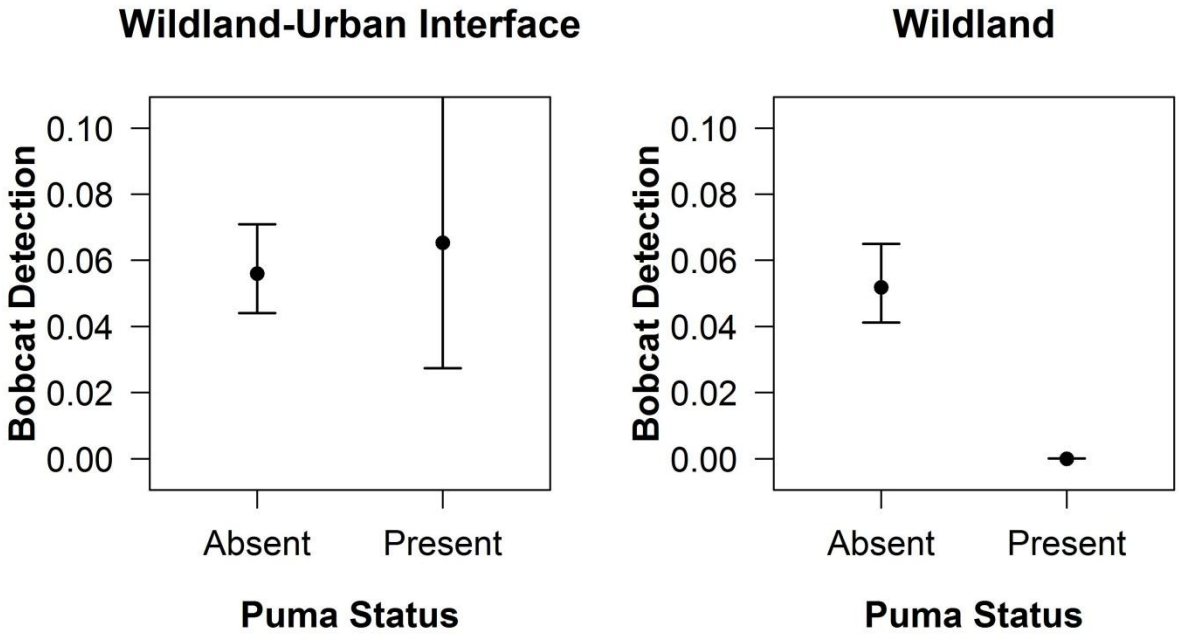


Figure 4b. FR daily bobcat detection probability

Figure 4. Bobcat daily detection probability estimates (with associated 95% confidence intervals) in relation to the absence and presence of pumas in exurban and wildland habitat on the Western Slope (WS) in 2009 (a) and wildland-urban interface (WUI) and wildland habitat on the Front Range (FR) in 2010 (b). Estimates are based on the interaction between Grid and Puma lag effect of 3 days on the WS (a) and the interaction between Grid and Puma lag effect of 2 days on the FR (b) using single-species occupancy models.

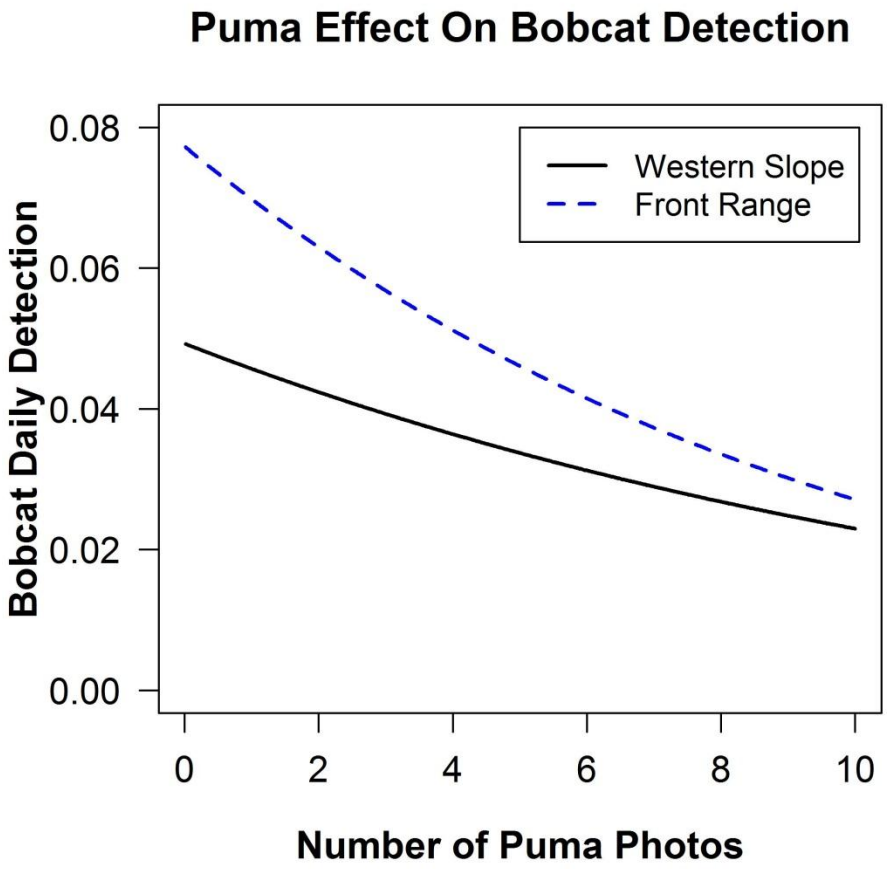


Figure 5. Bobcat detection probability decreased with the number of puma photographs at a site (i.e., Puma Count) on the Western Slope and Front Range of Colorado. Parameter estimates from the top models (Tables 5 and 6) were used to plot the relationship for Puma Count, Human Development (mean value), Grid 1, Puma lag effect (=0), and Puma lag effect interaction (=0). Our data for the number of puma photos (Puma Count) ranged from 0 - 8 on the WS and 0 - 6 on the FR.

LITERATURE CITED

Albrecht, M., and N. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134-141.

Beckmann, J. P., and J. Berger. 2003. Using black bears to test ideal-free distribution models experimentally. Journal of Mammalogy 84:594-606.

Beier, P., S. P. D. Riley, and R. M. Sauvajot. 2010. Mountain lions (Puma concolor). Pages 141-155 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban carnivores: ecology, conflict and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Bekoff, M. 2001. Observations of scent-marking and discriminating self from others by a domestic dog (Canis familiaris): tales of displaced yellow snow. Behavioural processes 55:75-79.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075-1085.

Birch, L. C. 1957. The meanings of competition. American Naturalist 91:5-18.

Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soulé. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7:552-563.

Boze, B. G. 2010. Correlates of coprophagy in the domestic dog (Canis familiaris) as assessed by owner reports. Journal of Applied Companion Animal Behavior 4:28-38.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, and M. Kinnaird. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4:75-79.

Caro, T., and C. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67-75.

Carothers, J. H., and F. M. Jaksić. 1984. Time as a niche difference: the role of interference competition. Oikos 42:403-406.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.

Cohen, J. E. 2003. Human population: the next half century. Science 302:1172-1175.

Creel, S., G. Spong, and N. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35-60 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, andR. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge, UK.

Crooks, K., S. Riley, S. Gehrt, T. Gosselink, and T. Van Deelen. 2010. Community ecology of urban carnivores. Pages 185-196 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban carnivores: ecology, conflict, and conservation. The John Hopkins University Press, Baltimore, MD, USA.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488-502.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London.

Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67:370-386.
Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399-407.
Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325-331.
Franklin, S., J. Troyer, J. Terwee, L. Lyren, W. Boyce, S. Riley, M. Roelke, K. Crooks, and S. Vandewoude. 2007. Frequent transmission of immunodeficiency viruses among bobcats and pumas. Journal of virology 81:10961-10969.
Gause, G. 1934. The struggle for existence. Williams and Wilkins, Baltimore, MD, USA.
Gehrt, S. D., S. P. Riley, and B. L. Cypher. 2010. Urban carnivores: ecology, conflict, and conservation. John Hopkins University Press, Baltimore, MD, USA.
George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107-117.
Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391:479-481.
Gorman, M. L., and B. J. Trowbridge. 1989. The role of odor in the social lives of carnivores. Pages 57-88 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, New York.
Hadidian, J., S. Prange, R. Rosatte, S. Riley, and S. Gehrt. 2010. Raccoons (Procyon lotor). Pages 35-47 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893-1905.
Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.
Hass, C. C. 2009. Competition and coexistence in sympatric bobcats and pumas. Journal of Zoology 278:174-180.
Heck, L., J. S. Lewis, and K. R. Crooks. 2014. Patterns of human recreation across rural and wildland-urban interface areas. In preparation.
Hines, J. E. 2006. Program PRESENCE. See http://www. mbrpwrc. usgs. gov/software/doc/presence/presence. html.
Karanth, K. U., J. D. Nichols, and N. S. Kumar. 2010. Estimating tiger abundance from camera trap data: field surveys and analytical issues. Pages 97-117 *in* A. F. O'Connell, J. D. Nichols, andK. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Tokyo, Japan.
Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy 72:391-396.
Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153-181.
Lenth, B. E., R. L. Knight, and M. E. Brennan. 2008. The effects of dogs on wildlife communities. Natural Areas Journal 28:218-227.
Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119-1139.

Lewis, J. S., and K. R. Crooks. 2014. Report to Boulder County Parks and Open Space: Day and night patterns of human recreation and effects on wildlife.
Lewis, J. S., K. A. Logan, M. W. Alldredge, L. L. Bailey, S. VandeWoude, and K. R. Crooks. 2014. Population density and occupancy of wild felids across a gradient of urbanization. Dissertation Chapter 1.
Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. Landscape and Urban Planning 101:99-107.
Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C.
MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.
MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, R. Andrew, J, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.
MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, CA.
Magle, S. B., V. M. Hunt, M. Vernon, and K. R. Crooks. 2012. Urban wildlife research: past, present, and future. Biological Conservation 155:23-32.
McDonnell, M. J., and A. K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23:1143-1155.
McDonnell, M. J., and S. T. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232-1237.
McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban ecosystems 11:161-176.
Meredith, M., and M. Ridout. 2013. Overlap. R Core Development Team.
Merkle, J., D. Stahler, and D. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56-63.
Nickerson, C., R. Ebel, A. Borchers, and F. Carriazo. 2011. Major uses of land in the United States, 2007. United States Department of Agriculture, Economic Research Service.
Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492-508.
Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? The American Naturalist 126:261-266.
Polfus, J. L., and P. R. Krausman. 2012. Impacts of residential development on ungulates in the Rocky Mountain West. Wildlife Society Bulletin 36:647-657.
Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual review of ecology and systematics 20:297-330.
R. Development Core Team 2014. R: a language and environment for statistical computing, Version 3.0.2. R Foundation for Statistical Computing. Vienna, Austria.
Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. Ecological Applications 15:799-805.

Ralls, K. 1971. Mammalian scent marking. Science 171:443-449.
Richmond, O. M., J. E. Hines, and S. R. Beissinger. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecological Applications 20:2036-2046.
Ridout, M., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322-337.
Riem, J. G., R. B. Blair, D. N. Pennington, and N. G. Solomon. 2012. Estimating mammalian species diversity across an urban gradient. The American midland naturalist 168:315-332.
Riley, S., E. Boydston, K. Crooks, and L. Lyren. 2010. Bobcats (Lynx rufus). Pages 121-138 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733-1741.
Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47:602-612.
Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011-1017.
Royle, A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.
Schneider, A., M. Friedl, and D. Potere. 2009. A new map of global urban extent from MODIS satellite data. Environmental Research Letters 4:1-11.
Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.
_____. 1982. The controversy over interspecific competition. American Scientist 70:586-595.
_____. 1983. Field experiments on interspecific competition. American Naturalist 122:240-285.
Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. A meta-analysis of global urban land expansion. PLoS One 6:1-9.
Soave, O., and C. Brand. 1991. Coprophagy in animals: a review. The Cornell Veterinarian 81:357-364.
Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, IL, USA.
Theobald, D. M. 2004. Placing exurban land-use change in a human modification framework. Frontiers in Ecology and the Environment 2:139-144.
Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society 10:1-34.
Theobald, D. M., and W. H. Romme. 2007. Expansion of the US wildland-urban interface. Landscape and Urban Planning 83:340-354.
Tracey, J. A., J. Zhu, E. Boydston, L. Lyren, R. N. Fisher, and K. R. Crooks. 2013. Mapping behavioral landscapes for animal movement: a finite mixture modeling approach. Ecological Applications 23:654-669.
Vaske, J. J., L. B. Shelby, and M. P. Donnelly. 2009. Estimating visitation to Boulder Open Space and Mountain Parks. (HDNRU Report No. 80) Report for Boulder Open Space and Mountain Parks: Colorado State University, Human Dimensions of Natural Resources.
Wiens, J. A. 1977. On competition and variable environment. American Scientist 65:590-597.

Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS One 8:e60590.
Wyatt, T. D. 2014. Pheromones and animal behaviour: chemical signals and signatures (second edition). Cambridge University Press, Cambridge, United Kingdom.

CONTACT NETWORKS REVEAL INTERSPECIFIC INTERACTIONS OF SYMPATRIC WILD FELIDS DRIVEN BY SPACE USE ALONG AN URBAN GRADIENT [3]

OVERVIEW

Competitive interactions between species are fundamental to understanding species assemblages, community dynamics, and ecological processes. Anthropogenic landscape change, particularly resulting from urbanization, can alter interspecific interactions; however, different forms of urbanization are predicted to have contrasting effects on competitive interactions. We developed contact networks between bobcats and pumas to (1) evaluate interspecific interactions between wild felids and (2) understand how competition varied among an urban gradient of low-density exurban development, wildland-urban interface, and wildland habitat. We used an extensive telemetry data set for bobcats and pumas across multiple study areas to evaluate *space-use overlap* (used to define potential interactions among animals) and three additional contact network metrics, including *degree* (number of potential interactions), *in-strength* (sum of space-use overlap for animals) and *equivalent social connectivity* (ESC; considering both space-use extent and the amount of space-use overlap). Regression analyses demonstrated that *space-use extent* was an important predictor of possible social interactions, where *space-use overlap*, *degree*, *in-strength*, and *ESC* generally increased with greater areas of space use. Counter to our predictions, felids associated with urbanized grids or with greater amounts of urbanization in their extent of space use did not appear to exhibit increased potential for interspecific interactions compared to animals in wildland areas or with low amounts of urbanization in their extents of space use. Bobcats appeared to have a greater opportunity to interact with female pumas based

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on *space-use overlap*, *degree*, and *in-strength*, but ESC was greater between bobcats and male pumas, likely due to the larger space-use extent by male compared to female pumas and the positive relationship between *space-use extent* and ESC. In addition, pumas and male bobcats exhibited a greater opportunity to interact, based on *space-use overlap*, *degree*, and *in-strength*, and demonstrated higher ESC compared to female bobcats. Greater ESC for male pumas and male bobcats suggests that males could be particularly important for facilitating connectivity of some ecological processes, such as the transmission of disease, through interspecific contact networks.

INTRODUCTION

Interactions among individuals are fundamental determinants of ecological communities, driving critical processes such as competition, predation, trophic cascades, disease spread, and ultimately the distribution and diversity of populations across fine to broad scales (MacArthur 1972, Rosenzweig 1995, Terborgh and Estes 2010). Landscape pattern, including that modified by anthropogenic activities, can shape animal distributions and competitive interactions and thus alters community-level processes (Forman 1995). In particular, urbanization can influence interactions of animals and lead to substantial impacts to ecological communities (Crooks and Soulé 1999, Faeth et al. 2005). Urbanization, ranging from low-density exurban to high-density urban development (Theobald 2005), currently covers hundreds of million acres globally (Schneider et al. 2009, Nickerson et al. 2011) and is projected to expand by hundreds of millions of acres in the next few decades (Cohen 2003, Theobald 2005, Seto et al. 2011). Understanding how urbanization influences community interactions is essential to manage and conserve animal populations in developed landscapes (Magle et al. 2012), for example as it relates to the spread

of pathogens and zoonotic diseases increasing in prevalence in landscapes modified by humans (Daszak et al. 2000, Bradley and Altizer 2007).

Carnivore populations can be especially impacted by anthropogenic landscape change, which can alter population characteristics, space-use patterns, and interactions within and between species (Crooks 2002, Gehrt et al. 2010). Although prior research has focused on intraspecific (i.e., within species) interactions of carnivores in urban systems (Gehrt et al. 2010), relatively few studies have evaluated how urbanization influences interspecific (i.e., between species) interactions within the carnivore community. The intensity of competition and intra-guild predation among carnivore species is predicted to vary along the landscape gradient of urbanization (Crooks et al. 2010). At the urban extreme of the gradient, characterized by small, isolated habitat fragments immersed within a human-dominated matrix, the intensity of interspecific interactions is predicted to be relatively low due to the loss of larger, dominant predators and simplification of the ecological community (i.e., refugia hypothesis). Interaction strength is expected to be moderate at the natural end of the urban gradient, characterized by landscapes with relatively few to no human residences, where dominant and subordinant predators can coexist broadly and exhibit some degree of spatio-temporal avoidance within areas of sympatry. The most intense interspecific interactions are expected to occur at intermediate levels of urbanization, characterized by large areas of natural habitat adjacent to the urban interface, where dominant predators can still persist, but habitat and resource limitations heighten overlap in space use and thus antagonistic encounters with subordinant species (i.e., pile-up hypothesis).

Within the Felidae family, pumas (i.e., mountain lion, cougar, panther; *Puma concolor*) and bobcats (*Lynx rufus*) are solitary with similar social and spatial organization; typically, adult

females have smaller home ranges that overlap little with neighboring females, whereas adult males have larger home ranges that typically overlap one to several females and sometimes neighboring males (Sandell 1989, Sunquist and Sunquist 2002). Across broad scales, the distribution of bobcats and pumas overlap extensively (Sunquist and Sunquist 2002) and both species overlap in their space use on finer scales in wildland habitat (Koehler and Hornocker 1991, Hass 2009). In addition, aggressive interactions occur between these felids and pumas will kill bobcats (Koehler and Hornocker 1991, Harveson et al. 2000). Both species are sensitive to anthropogenic disturbance but are also adaptable and able to persist in areas associated with urbanization (Crooks 2002, Beier et al. 2010, Riley et al. 2010). Bobcats and pumas typically occur at low population densities (Sandell 1989, Sunquist and Sunquist 2002); greater densities and overlap in space use between bobcats and pumas in areas influenced by urbanization could potentially lead to increased levels of competition, intra-guild predation, and cross-species disease transmission (Franklin et al. 2007, Crooks et al. 2010). For example, pumas acquired the bobcat strain of feline immunodeficiency virus (FIV) in urbanized California, presumably as a result of increased overlap of space use and contact rates near urban areas (Franklin et al. 2007). However, no empirical studies have explicitly evaluated how urbanization influences interspecific interactions among felids.

Social network analyses (i.e., contact networks, graph theory, network theory) provide a powerful tool to evaluate interactions among animals (Newman 2003, Craft and Caillaud 2011, Godfrey 2013), allowing comparisons of networks of animals in relation to anthropogenic factors (Wey et al. 2008). Various disciplines have created a variety of metrics within the network theory framework (e.g., social networks, landscape connectivity networks, technological networks) that might be applied to analyses of interactions among individuals. For example,

unique metrics developed in the landscape connectivity literature that consider both spatial extent and strength of connectivity, such as *probability of connectivity* (PC; Saura and Pascual-Hortal 2007) and *equivalent connectivity* (EC; Saura et al. 2011), have potential to be effectively applied to social network analysis by considering both space-use extent and the strength of interactions among individuals.

We developed contact networks between bobcat and puma populations to understand how interspecific interactions varied across a gradient of urbanization. Using an extensive telemetry data set, we evaluated interactions between bobcats and pumas across wildland, exurban development, and wildland-urban interface (WUI) habitat. Our analyses focused on 4 metrics including *space-use overlap* (used to define potential interactions among animals), *degree* (number of potential interactions for animals), *in-strength* (sum of space-use overlap for animals), and *equivalent social connectivity* (ESC; considering space-use extent and overlap between animals). We tested specific predications regarding (1) patterns of potential interspecific interactions between bobcats and pumas and (2) how *space-use overlap*, *degree*, *in-strength*, and ESC might change along the urban gradient at both the population and individual level. For each species, we predicted a positive relationship between the extent of space use for an animal and the number of interspecific interactions. Further, we expected that male pumas, given their larger home ranges (Logan and Sweanor 2001), would interact with a greater number of bobcats, but that female pumas would exhibit greater spatial overlap and *in-strength* with bobcats due to a more similar spatial scale in their extents of space use. Similarly for bobcats, we expected males to interact with a greater number of pumas, compared to females, and exhibit greater *space-use overlap* and *in-strength* due to more similar scales in their extents of space use. We also predicted that because males would use areas of greater spatial extent and interact with a

greater number of felids, their ESC would be greater than females. At both the population and individual levels, we expected elevated opportunities for interspecific interactions in urbanized landscapes as predicted by the pile-up hypothesis (Crooks et al. 2010), specifically within exurban development and WUI habitat compared to wildland areas.

STUDY AREA

We conducted our research across two study areas in Colorado, USA that exhibited varying degrees of urbanization and human influence. In 2009-2010, we worked on the Western Slope (WS) of Colorado on the Uncompahgre Plateau near the towns of Montrose and Ridgway (Figure 1). Common vegetation included pinyon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), gambel oak (*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). We divided the WS study site into two sampling grids. The southern grid 1 sampled low-density residential development on Log Hill Mesa (population = 1,041; US Census Bureau 2010); residential parcel sizes were distributed, from most to least numerous, across 5 acre, 2 acre, 1 acre, ≥ 5 acre, and ≥ 40 acre properties. Within areas of exurban development, travel corridors of natural habitat and open space property, often with associated recreation trails, were present. The northern grid 2 sampled primarily undeveloped, wildland habitat, although some small areas of low-density human residences and hunting camps occurred on or near the grid.

In 2010 - 2012, we worked on the more urbanized Front Range (FR) of Colorado (Figure 1). Common vegetation included ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), juniper, aspen, and mountain mahogany (*Cercocarpus montanus*). A network of open space properties with recreational trails occurred across the study area. Similar to the WS, we divided the FR

study area into two sampling grids. The southern grid 1 occurred adjacent to the wildland-urban interface associated with the city of Boulder (population = 97,385, US Census Bureau 2010) and was characterized by open-space properties with some human residences on or near the grid. The northern grid 2 occurred across undeveloped public properties, although a small number of rural human residences occurred on private property inholdings. See Lewis et al. (2014c) for an expanded description of the study area.

METHODS

Animal Capture and Telemetry Data

Bobcats were captured in black metal-wire cage traps (40 x 55 x 100 cm) with attractants from mid-June through March 2009 – 2011. All cage traps were fit with very high frequency (VHF) trap transmitters (Telonics Inc., Mesa, AZ, USA) that indicated when trap doors closed. Captured bobcats were immobilized through hand-injection of a combination of Ketamine (10.0 mg/kg) and Xylazine (1.0 mg/km), and Yohimbine (0.125 mg/km) was used to reverse Xylazine (Kreeger et al. 2002). We fit GPS collars (210 – 280 g, Telemetry Solutions, Concord, CA, USA) with timed drop-off mechanisms and degradable cotton spacers along the collar belting on adult-sized bobcats. GPS collars were programmed to record locations on the WS every 5-7 hours and on the FR every 3-4 hours. GPS collars were also equipped with VHF beacons that lasted up to 2 years, which allowed for the continued monitoring of animals to assess site fidelity to an area. Bobcats were weighed, sex was recorded, and age was estimated based on tooth development (Crowe 1975), wear, and coloration. Pumas were captured from 2005 – 2011 with the use of hounds and baited cage traps, immobilized with Telazol (5.0 – 9.0 mg/kg), and fit with GPS collars (Lotek, Newmarket, Ontario, Canada; Northstar, King George, VA, USA;

Vectronics, Berlin, Germany) programmed to record a location every 5-7 hours on the WS and 3-4 hours on the FR. To increase the duration of time that location data were acquired for pumas on the WS, some individuals were fit with VHF collars (Lotek) and aerial positional locations were obtained approximately every 2 weeks. Pumas were also weighed, fit with eartags, and age and sex were recorded. Methods for animal capture were approved by the Colorado State University Animal Care and Use Committee (11-2453A).

Contact Networks and Metrics

To evaluate interspecific interactions, we estimated space use for each individual fit with a telemetry collar and then calculated four metrics using these data. First, we estimated *space-use overlap* among all individuals and used this information to calculate three additional contact network metrics: *degree*, *in-strength*, and *equivalent social connectivity*.

Telemetry data were used to estimate space use for felids that occurred on our sampling grids from June 2009 to June 2010 on the WS and September 2010 to September 2011 on the FR. Motion-activated cameras also operated during these periods of time (for additional details see Lewis et al. 2014c) and assisted in evaluating which animals occurred on our sampling grids and assessing site fidelity of animals during our study. For animals known to occur on our grids during the focal periods, telemetry data before and after focal periods were used, if necessary, to estimate space use for an entire year (e.g., if telemetry data collection began in November 2010 for an animal, then space use would be estimated through October 2011). Because felids exhibit spatial fidelity (Sunquist and Sunquist 2002), we assumed that space use immediately before or after our focal period was similar and thus representative to that during focal periods. In addition, for animals in which data were unavailable for an entire year, estimates of space use were assumed to be representative for annual periods; although GPS locations might be

unavailable for some animals over annual periods (due to GPS battery expiration), VHF tracking of those animals enabled continued monitoring to assess whether individuals maintained site fidelity to an area. Each individual was assigned to the grid with the greatest proportion of its telemetry locations (for further description about time spent on grid techniques see Lewis et al. 2014c). One male bobcat (i.e., M5) on the FR left the study area immediately after being captured and fit with a GPS collar, thus this individual was excluded from analyses.

Space-use patterns of individuals were calculated by estimating the utilization distribution (UD) using telemetry locations of animals. For animals fit with GPS collars (bobcats n = 37; pumas n = 25), UDs were estimated with the Brownian bridge movement model (BBMM) (Horne et al. 2007) at 30 m resolution with the mkde package (Tracey 2014) in program R (R Development Core Team 2014). The BBMM is appropriate to use with fine-scale GPS data sets because it is designed to be used with temporally correlated telemetry locations, incorporates information about animal movement into estimates of space-use, and tends to not over-smooth or under-smooth space-use extent (Horne et al. 2007, Walter et al. 2011a). For pumas on the WS fit with VHF collars (n = 4), because data that was not temporally correlated (i.e., independent locations obtained approximately 2 weeks apart), UDs were estimated with the kernel home range estimator using likelihood cross validation (Horne and Garton 2006) in the Animal Space Use package (Horne and Garton 2009). We used the 99% cumulative probability of space use for all analyses.

Both indirect (amount of shared space use) and direct (number of physical contact between animals) measures of interactions are important for understanding patterns of competition, predation, and disease transmission and can be positively correlated (Vander Wal et al. 2014), including for solitary carnivores (Robert et al. 2012). To evaluate the opportunity for

individuals to interact, we estimated *space-use overlap* among animals (Godfrey et al. 2010, Robert et al. 2012, Vander Wal et al. 2014) using the utilization distribution overlap index (UDOI) because this metric is most appropriate for evaluating the sharing of space use (Fieberg and Kochanny 2005). Values of UDOI can range from 0 (no overlap) to >1 (if nonuniform UDs exhibit a high degree of overlap). Specifically, UDOI has a strong positive correlation with contact rates for solitary carnivores (Robert et al. 2012). UDOI was calculated with user-created code with the package raster (Hijmans 2014) in program R (R Development Core Team 2014). Space-use overlap for an individual was calculated by averaging space-use overlap with all individuals.

Contact networks represent individual animals as nodes and connections between individuals as edges to evaluate social interactions (Newman 2003). We defined potential interspecific interactions between two animals if their UDs overlapped (Godfrey et al. 2010, Vander Wal et al. 2014). Covariates can be applied to nodes and edges, such as the size of the node (i.e., extent of individual space use) and edge weight (i.e., amount of space-use overlap). To create figures of contact networks and visualize animal interactions, we used the igraph package (Csardi 2014) in program R (R Development Core Team 2014). *Degree* measures the number of edges connected to an individual (Newman 2003), which reflects the number of animals with which an individual potentially interacts (Wey et al. 2008). The edge weight (i.e., relationship strength, which we defined based on space-use overlap using the UDOI statistic, as explained above) evaluates the potential for repeated interactions (Wey et al. 2008). Edge weights were used to calculate *in-strength*, which is the sum of all weighted edges associated with an individual, and can effectively measure interaction strength among animals (Godfrey et al. 2010).

The *equivalent connectivity* (EC) metric, originating from landscape ecology, evaluates how habitat patch size and connectedness affects landscape connectivity. EC is defined as the size of a single patch (maximally connected) that would provide the same probability of connectivity as the actual habitat pattern in the landscape (Saura et al. 2011). Larger habitat patches are more effective than smaller patches in maintaining biodiversity, and more connected habitat patches facilitate the flow of ecological processes, including animal movement, through the landscape (Forman 1995, Rosenzweig 1995, Crooks and Sanjayan 2006). Thus, with the EC metric, larger habitat patches that are well connected to other patches result in greater landscape connectivity. Here we apply the EC metric analogously to contact networks where individuals with greater space-use extents encounter more of the landscape and likely interact with more individuals, and increased overlap in space use between animals can increase potential interactions.

Thus, within a contact network framework, we interpreted the EC metric as:

$$\text{EC} = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \, a_j p_{ij}^*}$$

where a_i and a_j are the spatial extents of space use for animals *i* and *j*, and p_{ij}^* is the probability of two animals interacting. We defined p_{ij}^* as the overlap in space use between animals *i* and *j* using the Bhattacharyya's affinity (BA) statistic (Fieberg and Kochanny 2005) because it ranged from 0 to 1 and was thus more appropriate to use with the EC metric compared to the UDOI statistic, which can be >1; each of these metrics effectively rank animals relative to their amount of space-use overlap and are based on the joint distribution for 2 animals (i.e., the product of the 2 UDs; Fieberg and Kochanny 2005). We calculated BA with user-defined code in the package *raster* (Hijmans 2014) in program R (R Development Core Team 2014). Because we were interested in evaluating equivalent connectivity for individual animals, we simplified the EC

metric to calculate, what we refer to as, *equivalent social connectivity* (ESC) for an individual animal (ESC_i) as follows:

$$ESC_i = \sqrt{\sum_{j=1}^{n} a_i \, a_j p_{ij}^*}$$

where a_i is the space-use extent for the focal animal *i* and a_j are the spatial extent of space use for animals *j* and p_{ij}^* is the BA value of space-use overlap between animals *i* and *j*. We defined ESC as the relative potential for an individual to contribute to the flow of particular ecological processes that are influenced by both space-use overlap and extent. Thus, whereas degree and in-strength focus solely on edge characteristics to index individual interactions, ESC considers the attributes of both nodes (space-use extent) and edges (space-use overlap) to evaluate connectedness of animals. The additional node information is expected to better represent connectivity of some ecological processes between animals. Because ESC explicitly incorporates information about space-use extent, we expected these two metrics to be positively related. However, if larger extents of space use resulted in very low or variable levels of space-use overlap with neighbors, then the slope of the relationship between space-use extent and ESC could be negative or zero. We defined social interactions as direct or indirect contacts occurring between animals, including both intra- (e.g., Seidensticker et al. 1973, VanderWaal et al. 2014) and interspecific interactions (Morse 1974).

Statistical Analyses

Group-Level Evaluation: Sex and Urbanization

For all metrics, we first calculated values for each individual animal and then averaged across individuals to estimate means and standard errors. To compare interactions between groups of animals, we used two-sample t-tests in program R (R Development Core Team 2014) to test for differences in contact metric values between males and females and forms of

urbanization (exurban development and wildland habitat on the WS and wildland-urban interface and wildland habitat on FR) within each study area.

Individual-Level Evaluation

Regression analyses were used to evaluate how individuals responded to urbanization within their extents of space use. All regression analyses were conducted in R (R Development Core Team 2014). We used simple linear regression to evaluate the relationship between the space-use extent of animals and the number of potential interspecific interactions (i.e., *degree*) with neighboring individuals.

We used multiple regression to evaluate how urbanization within an individual animal's extent of space use influenced their interspecific contacts. Response variables as defined by contact network metrics (i.e., *space-use overlap*, *degree*, *in-strength*, and ESC) were evaluated in relation to a suite of predictor variables, including *Sex* (male or female for focal individual), *grid*, *space-use extent*, and *human development*. The covariate *grid* compared interactions for animals associated with either exurban development and wildland areas (on the WS) or wildland-urban interface and wildland areas (on the FR). The covariate *human development* characterized the amount of human influence associated with each animal's extent of space use. We created a human development layer where each human occurrence point (HOP; residence or structure) across study areas was digitized as a point using ArcGIS v10 software (ESRI, Redlands, CA, USA) from color orthophotos (1-m resolution). Using Arc Toolbox in ArcMap10, we fit a Gaussian kernel with a radius of 1000m over each HOP, where the density, or influence, was greatest directly at the point of interest and decreased out to the specified radius of a circle. A radius of 1000m was used to predict the potential extent of disturbance from humans and urbanization on animals, as previous research reported animals responding to human disturbance

at this distance (e.g., Siikamäki and Kangas 2009, Donovan et al. 2011, Hamer and Parris 2011). The extent of space use for each individual was intersected with the GIS layer of Human Development and we summed the total amount of human development within each animal's extent of space use. Each continuous covariate was standardized by subtracting the sample mean from the input variable values and dividing by the standard deviation (Schielzeth 2010). Covariates were evaluated for multicollinearity using Pearson's correlation and considered correlated if $r > 0.6$; *sex* was highly correlated with *space-use extent* ($r = 0.62$), where males consistently exhibited larger extents of space use than females, and we subsequently excluded Sex from modeling. For each response variable, we evaluated model sets comprised of all possible combinations of covariates for each species in each study area and ranked models using Akaike's Information Criteria corrected for small sample size (AIC_c) (Burnham and Anderson 2002). To evaluate the importance of variables in models we calculated variable importance values (VIV) and model averaged parameter estimates across models in which they occurred (Burnham and Anderson 2002).

RESULTS

We used telemetry data from 19 bobcats and 10 pumas on the WS and 18 bobcats and 19 pumas on the FR to estimate space use, create contact networks (Figure 2), and evaluate contact network metrics. Figure 2 provides a visual summary of contact network metrics, including *space-use overlap*, *degree*, *in-strength* in relation to space-use extent for bobcats and pumas on the WS and FR. Figure 3 provides an example of *space-use overlap* between pumas and bobcats.

Group-Level Evaluation: Sex

Bobcats exhibited greater potential to interact with female pumas compared to male pumas, as indexed by *space-use overlap*, *degree*, *in-strength* (Table 1). As predicted, bobcats demonstrated greater overlap in space use with female pumas, interacted with a greater number of female pumas (i.e., *degree*), and exhibited greater *in-strength* with female pumas, compared to male pumas, across both the WS and FR (Table 1). However, bobcats had greater *equivalent social connectivity* (ESC) with male compared to female pumas (Table 1).

Pumas exhibited greater potential to interact with male bobcats compared to female bobcats (Table 1). In general, pumas demonstrated greater *space-use overlap* with male bobcats, interacted with a greater number of male bobcats (i.e., degree), and exhibited greater *in-strength* with male bobcats, compared to female bobcats, across both the WS and FR (Table 1). In addition, pumas exhibited greater ESC with male compared to female bobcats (Table 1).

Group-Level Evaluation: Urbanization

Counter to our predictions, urbanization did not appear to notably alter interspecific contact networks between bobcats and pumas across our two study sites. In both the WS and FR, felids demonstrated similar patterns of *space-use overlap*, interacted with similar numbers of individuals (i.e., *degree*), exhibited similar *in-strength*, and had similar ESC values (Table 2) in urbanized (WS exurban; FR WUI) versus wildland grids. Thus animals associated with urbanized and wildland areas appeared to demonstrate similar patterns of potential interspecific interactions.

Individual-Level Evaluation

Potential interspecific interactions for individual animals was best explained by *space-use extent*, where individuals with larger extents of space use exhibited greater *space-use overlap*,

degree, *in-strength*, and ESC (Table 3; Appendices Tables 1 – 16). As predicted, there was a positive relationship between the extent of space use for bobcats and pumas and the number of potential interspecific contacts (i.e., *degree*) on the WS and FR (Figure 4). Counter to our predictions, animals with greater amounts of human development within their extents of space use did not appear to exhibit greater levels of interspecific interactions, based on low VIV and model rankings, and 95% confidence intervals for parameter estimates overlapping 0 for covariates of urbanization (Table 3; Appendices 1 – 16). In general, *space-use extent* exhibited high VIV across models and the anthropogenic variables *grid* and *human development* had little support in our models. However, pumas with smaller extents of space use exhibited greater *space-use overlap* and *in-strength* with bobcats, likely due to more concentrated use of shared areas (Table 3). Also, ESC of pumas on the WS was positively influenced by *human development*, with a high VIV and 95% confidence interval that did not overlap 0, possibly due to animals with larger extents of space use encountering a greater number of human residences. However, *human development* within an animal's extent of space use appeared to be a poor predictor in all other analyses (Table 3; Appendices 1 – 16).

DISCUSSION

The potential for interspecific interactions between bobcats and pumas varied by extent of space use and sex but, counter to our predictions, appeared to be similar between groups of animals associated with urbanized and wildland areas and animals with greater amounts of human development within their extents of space use. For each species, *space-use overlap*, number of potential interactions for animals (i.e., *degree*), sum of space-use overlap for animals (i.e., *in-strength*), and *equivalent social connectivity* (ESC; considering space-use extent and the

amount of space-use overlap between animals) generally increased with the extent of space use for individuals.

Across study areas, bobcats tended to exhibit a greater opportunity to interact with female pumas, as indexed by *space-use overlap*, *degree*, and *in-strength*. This result highlights that relative scale of space use might be an important driver of interspecific interactions, with female pumas exhibiting small space-use extents that were more comparable to that of bobcats. ESC, however, was greater with male pumas, likely due to the large extents of space use of male compared to female puma and the positive relationship between *space-use extent* and ESC. Male pumas are more likely to exhibit aggressive behavior towards other pumas, including within-species mortality (Logan and Sweanor 2001, Logan and Sweanor 2010); if this aggression also translates across species, then male pumas might be more likely to exhibit intra-guild predation towards bobcats as well. Our results also suggest that pumas were more likely to interact with male bobcats, as indexed by *space-use overlap*, *degree*, and *in-strength*, again likely because male bobcats exhibited greater space-use extents that were more similar in scale to that of pumas. Similarly, pumas demonstrated the greatest ESC with male compared to female bobcats, again likely due to the large extents of space use of male bobcats.

Based on our results, ecological factors leading to greater space-use extents for animals would be predicted to increase the opportunity for interactions. For felids, greater extents of space use are often related to sex, where males have larger home ranges compared to females, and resident and transient animals, where transient animals often exhibit greater extents of space use when trying to establish a home range (Sunquist and Sunquist 2002). However, transient and resident animals can exhibit different types of behaviors (e.g., mating or fighting to maintain or obtain a home-range), which could be important in understanding the types of social encounters

experienced during interactions. In addition, patterns of felid space use are related to food availability both spatially (Ferguson et al. 2009) and temporally (Knick 1990) where home-range size increases with reduced prey, which can be influenced by environmental conditions. Competition might also potentially increase extents of space use if subordinate animals are forced to travel more due to displacement by superior competitors (interference competition) or if resources are depleted in an area (exploitation competition).

Anthropogenic factors also can be important determinants of animal space use. In particular, urbanization can influence both space-use extent and animal interactions (Gehrt et al. 2010). Space-use extent can be positively correlated with levels of urbanization in felids, where greater amounts of urbanization within an individual's home range are related to larger extents of space use (Riley et al. 2003). It is unclear, however, if greater levels of urbanization reduce habitat quality and thus require animals to use larger spatial extents to fulfill life-history requirements, such as food acquisition, or if animals with larger home ranges simply are more likely to encounter areas of urbanization due to greater movement extents. In addition, some estimates of space use, such as the Minimum Convex Polygon, can be particularly prone to overestimate space use by incorporating non-used areas, especially if animals demonstrate irregular boundaries of space use (Burgman and Fox 2003). Estimates of space use that consider the utilization distribution and minimize overestimating space use into unused areas will likely provide more reliable results of spatial extent, especially in heterogeneous landscapes influenced by patterns of urbanization.

Conversely, greater levels of urbanization are reportedly related to decreased home range size (Riley 2006, Hadidian et al. 2010, Soulsbury et al. 2010) and increased overlap in space use among individuals (Riley et al. 2006) in some urban carnivores. The home-range pile-up

hypothesis predicts that animals adjacent to anthropogenic barriers exhibit greater amounts of space-use overlap, population density, and interactions due to restricted dispersal (Riley et al. 2006, Crooks et al. 2010). However, at both population and individual levels, neither species in our study appeared to exhibit increased opportunities for interactions in relation to greater amounts of urbanization. *Space-use overlap*, *degree*, and *in-strength* were not greater for animals associated with habitat influenced by urbanization compared to wildland areas or for animals with greater amounts of urbanization with their extents of space use. Further, population density for bobcats and pumas in our study areas was not greater in habitat influenced by urbanization (Lewis et al. 2014c). Home-range pile-up might be observed for specific age and sex classes within populations (e.g., adult females; Riley et al. 2006), but our sample sizes did not allow for such evaluations and this would be an important area of future study. In addition, increased interactions might be more likely to occur in landscapes more fragmented than our study area, such as in habitat patches completely surrounded by urbanization, where animal dispersal opportunities are greatly reduced or eliminated (e.g., fence effect; Krebs et al. 1969, Adler and Levins 1994).

Although contact network analyses suggested that animals associated with urbanized habitat did not appear to exhibit elevated potential for interaction compared to animals in wildland habitat, bobcats and pumas clearly respond to urbanization both behaviorally and numerically. Both felids can be adaptable to human disturbance (Beier et al. 2010, Riley et al. 2010), but, bobcats and pumas avoid using areas with high density urbanization (Dickson and Beier 2002, Riley et al. 2010), are less likely to be detected as human disturbance from residences increases (Lewis et al. 2014a), and alter their movement patterns to avoid anthropogenic disturbance (Tracey et al. 2013, Wilmers et al. 2013). In addition, increased risks

of mortality, such as those resulting from vehicle collisions, toxicants, and human-wildlife conflicts, are associated with urbanized areas for both felids (Beier et al. 2010, Burdett et al. 2010, Riley et al. 2010). Ultimately, urbanization can influence population abundance and density of felids; in our study area, population densities for both bobcats and pumas were estimated to be lower in exurban development compared to wildland habitat (Lewis et al. 2014c). Felids might respond to areas of urbanization as non-habitat or habitat of lower suitability similarly to other land cover types that are less preferred.

Despite animals tending to avoid human residences, when animals do use habitat directly influenced by urbanization, the opportunity for interactions can vary depending upon spatial and temporal scale. Across broad seasonal scales, other research demonstrated in this study area that pumas did not exclude bobcats from urbanized or wildland areas and urbanization did not alter the interactions between bobcats and pumas (Lewis et al. 2014a). However, at finer temporal scales, bobcats were less likely to be detected at sites recently visited by pumas (up to a few days), but only in wildland habitat; in habitat associated with urbanization, bobcats did not appear to temporally avoid pumas at fine scales, thus increasing the opportunity for interspecific interactions (Lewis et al. 2014a). Our research evaluating interspecific interactions using contact networks can be considered a broad-scale analysis focusing on overall patterns of space use across annual periods. Analyses evaluating direct interactions among animals could provide finer scale results of interspecific interactions. Direct interactions could be analyzed using high resolution GPS data or proximity collars (e.g., Hamede et al. 2009) to evaluate the distribution of locations that are concurrent in space and time, thus providing a more refined index of potential contacts. Although overlap in space use and direct contacts can be correlated for solitary carnivores (Robert et al. 2012), the relationship between space-use overlap and contact rates can

be variable (Schauber et al. 2007). It would be predicted that finer-scale direct contacts between species might vary depending on animal behavior and landscape characteristics influenced by urbanization (e.g., Crooks et al. 2010). Our study evaluated interspecific interactions occurring in habitat influenced by two forms of urbanization (i.e., exurban development and wildland-urban interface habitat) and future work could evaluate interactions across other forms or urbanization (e.g., rural, suburban, and urban habitat). Lastly, additional human impacts across the gradient of urbanization, such as recreation (Knight and Gutzwiller 1995), roads (Forman et al. 2002), and energy development (Naugle and Boyce 2011), could impact space use by animals and potentially affect interactions among species.

Contact networks provide a powerful tool to investigate potential interactions among animals and there is increasing emphasis on applying contact network analyses to wildlife populations for management and conservation (Wey et al. 2008). Although much research has focused on using contact networks to evaluate questions investigating disease transmission in animals (Craft and Caillaud 2011, Godfrey 2013), this framework can also be used to ask more general ecological questions about social relationships within and between species (Wey et al. 2008). There are limitations, however, to be considered when evaluating contact network metrics. In telemetry studies, it is very challenging, if not impossible, to fit all animals with tracking collars and thus contact network metrics reflect the sampled population and likely an incomplete analysis of interactions among all individuals in a population; although reduced sample size can provide robust results (Wey et al. 2008). In addition, contact network metrics are dependent upon the spatial distribution of collared animals relative to the sampled population, which can result in boundary effects (Craft et al. 2009). Although metrics evaluating the importance of nodes within a network, such as centrality, closeness centrality, and

betweenness centrality, can provide valuable information about network structure (Newman 2003), such metrics can be sensitive to small sample size and node position within the network (Wey et al. 2008) and were not considered in our analysis. However, contact network metrics can be robust to small sample sizes (Wey et al. 2008) and we used metrics and analyses that aimed to minimize such limitations.

Overall, our study demonstrated how contact networks can provide valuable insight into interspecific interactions, including the importance of space-use extent and sex in evaluating the potential for competitive interactions and intra-guild predation in developing landscapes. In particular, greater ESC for male pumas and male bobcats suggests that males could be particularly impactful for facilitating connectivity of particular ecological processes, such as the transmission of disease, through contact networks.

Table 1. Contact network statistics evaluating interactions between bobcats and pumas on the Western Slope (WS) and Front Range (FR) of Colorado. See Methods for further description of metrics.

Study	Evaluation			Space-Use Overlap[b]		Degree[c]		In-strength[d]			Equivalent Social Connectivity[e]	
Area	Focal Group	n[a]	Comparative Group	Mean (se)	Range	Mean (se)	Range	Mean (se)	Range	Sum	Mean (se)	Range
WS	Bobcats	19	Pumas	0.064 (0.015)	0.014 - 0.183	6.42 (0.18)	5 - 8	0.41 (0.06)	0.10 - 1.28	7.75	100.45 (11.22)	57.67 - 243.61
WS			Puma Males	0.030 (0.007)[1*]	0.006 - 0.131	2.68 (0.11)[2*]	2 - 3	0.08 (0.02)[3*]	0.02 - 0.39	1.48	84.85 (9.67)[4*]	47.62 - 203.91
WS			Puma Females	0.092 (0.021)[1*]	0.014 - 0.223	3.74 (0.15)[2*]	2 - 5	0.33 (0.04)[3*]	0.06 - 0.89	6.27	53.17 (6.00)[4*]	27.60 - 133.29
WS	Pumas	10	Bobcats	0.069 (0.020)	0.008 - 0.201	12.30 (1.72)	2 - 19	0.78 (0.20)	0.03 - 2.21	7.76	134.28 (24.60)	23.25 - 263.16
WS			Bobcat Males	0.076 (0.017)[5]	0.011 - 0.159	6.60 (0.93)[6]	1 - 10	0.46 (0.09)[7]	0.02 - 0.85	4.57	113.74 (21.61)[8]	22.15 - 229.16
WS			Bobcat Females	0.062 (0.026)[5]	0.004 - 0.273	5.70 (0.80)[6]	1 - 9	0.32 (0.13)[7]	<0.01 - 1.36	3.19	68.97 (13.26)[8]	7.06 - 141.80
FR	Bobcats	18	Pumas	0.075 (0.013)	0.002 - 0.160	10.89 (0.65)	6 - 15	0.88 (0.18)	0.01 - 2.40	15.90	119.25 (15.40)	30.83 - 228.13
FR			Puma Males	0.055 (0.015)[9]	<0.001 - 0.232	4.00 (0.27)[10*]	1 - 5	0.24 (0.06)[11*]	<0.01 - 0.86	4.28	94.95 (13.31)[12]	11.90 - 185.50
FR			Puma Females	0.089 (0.017)[9]	0.001 - 0.219	6.89 (0.52)[10*]	3 - 10	0.65 (0.15)[11*]	<0.01 - 2.11	11.61	69.66 (8.99)[12]	23.39 - 137.41
FR	Pumas	19	Bobcats	0.086 (0.014)	0.003 - 0.254	10.32 (0.93)	3 - 18	0.84 (0.16)	0.03 - 3.31	15.89	109.61 (17.12)	32.96 - 351.92
FR			Bobcat Males	0.102 (0.029)[13]	0.003 - 0.490	6.79 (0.67)[14*]	2 - 12	0.61 (0.17)[15*]	0.02 - 3.19	11.51	95.46 (15.78)[16*]	32.39 - 307.76
FR			Bobcat Females	0.067 (0.019)[13]	<0.001 - 0.267	3.53 (0.32)[14*]	1 - 6	0.23 (0.06)[15*]	<0.01 - 0.80	4.39	47.31 (9.00)[16*]	1.56 - 170.69

[a] Number of focal individuals

[b] Space-use overlap is the overlap of utilization distributions among animals

[c] Degree is the number of connections to other individuals

[d] In-strength is the sum of spatial overlap with all individuals

[e] Equivalent social connectivity considers space-use extent and amount of space-use overlap among individuals

[1 - 16] Statistical tests were conducted between values with the same reference number. A star * indicates significance at a p-value of 0.05.
1 ($t = -4.13$, $df = 27.72$, $p < 0.001$); 2 ($t = -5.67$, $df = 32.96$, $p < 0.001$); 3 ($t = -5.14$, $df = 25.43$, $p < 0.001$); 4 ($t = 2.78$, $df = 30.08$, $p = 0.009$);
5 ($t = 0.45$, $df = 15.56$, $p = 0.66$); 6 ($t = 0.73$, $df = 17.61$, $p = 0.47$); 7 ($t = 0.87$, $df = 16.64$, $p = 0.39$); 8 ($t = 1.76$, $df = 14.94$, $p = 0.10$);
9 ($t = -1.50$, $df = 33.08$, $p = 0.14$); 10 ($t = -4.96$, $df = 25.53$, $p < 0.001$); 11 ($t = -2.50$, $df = 21.94$, $p = 0.02$); 12 ($t = 1.57$, $df = 29.84$, $p = 0.13$);
13 ($t = -1.02$, $df = 31.64$, $p = 0.32$); 14 ($t = 4.44$, $df = 25.39$, $p < 0.001$); 15 ($t = 2.10$, $df = 22.37$, $p = 0.047$); 16 ($t = 2.65$, $df = 28.60$, $p = 0.01$)

Table 2. Contact network statistics evaluating interactions between bobcats and pumas across different forms or urbanization on the Western Slope (WS) and Front Range (FR) of Colorado. See Methods for further description of metrics.

Study	Focal with Comparitive			Space-Use Overlap[b]		Degree[c]		In-strength[d]			Equivalent Social Connectivity[e]	
Area	Group Evaluation	n[a]	Grid	Mean (se)	Range	Mean (se)	Range	Mean (se)	Range	Sum	Mean (se)	Range
WS	Bobcats with Pumas	10	Exurban	0.059 (0.009)[1]	0.021 - 0.120	6.50 (0.22)[2]	5 - 7	0.38 (0.05)[3]	0.15 - 0.72	3.78	87.51 (5.94)[4]	57.67 - 117.69
WS	Bobcats with Pumas	9	Wildland	0.068 (0.016)[1]	0.014 - 0.183	6.33 (0.29)[2]	5 - 8	0.44 (0.11)[3]	0.10 - 1.28	3.97	114.84 (22.47)[4]	73.02 - 243.61
WS	Pumas with Bobcats	3	Exurban	0.117 (0.050)[5]	0.028 - 0.201	10.67 (0.88)[6]	9 - 12	1.22 (0.54)[7]	0.33 - 2.21	3.65	141.30 (45.45)[8]	91.98 - 232.09
WS	Pumas with Bobcats	7	Wildland	0.049 (0.015)[5]	0.008 - 0.123	13.00 (2.44)[6]	2 - 19	0.59 (0.15)[7]	0.03 - 1.11	4.11	131.28 (31.57)[8]	23.25 - 263.16
FR	Bobcats with Pumas	10	WUI	0.075 (0.017)[9]	0.019 - 0.197	11.67 (1.05)[10]	6 - 15	0.94 (0.27)[11]	0.24 - 2.40	8.46	112.59 (22.05)[12]	30.83 - 218.93
FR	Bobcats with Pumas	9	Wildland	0.075 (0.020)[9]	0.002 - 0.158	10.11 (0.72)[10]	7 - 14	0.83 (0.26)[11]	0.01 - 2.21	7.43	125.90 (22.60)[12]	62.55 - 228.12
FR	Pumas with Bobcats	12	WUI	0.086 (0.014)[13]	0.019 - 0.197	9.42 (1.28)[14]	3 - 18	0.71 (0.10)[15]	0.13 - 1.23	8.53	98.63 (24.31)[16]	32.96 - 351.92
FR	Pumas with Bobcats	7	Wildland	0.085 (0.031)[13]	0.003 - 0.254	11.86 (1.16)[14]	8 - 17	1.05 (0.42)[15]	0.03 - 3.31	7.37	128.43 (20.90)[16]	57.97 - 193.79

[a] Number of focal individuals

[b] Space-use overlap is the overlap of utilization distributions among animals

[c] Degree is the number of connections to other individuals

[d] In-strength is the sum of spatial overlap with all individuals

[e] Equivalent social connectivity considers space-use extent and amount of space-use overlap among individuals

[1 - 16] Statistical tests were conducted between values with the same reference number. No tests were significant at a p-value of 0.05.
1 (t = -0.52, df = 12.78, p = 0.61); 2 (t = 0.46, df = 15.52, p = 0.65); 3 (t = -0.51, df = 11.36, p = 0.62); 4 (t = -1.17, df = 9.12, p = 0.27);
5 (t = 1.31, df = 2.36, p = 0.30); 6 (t = -0.90, df = 7.30, p = 0.40); 7 (t = 1.11, df = 2.33, p = 0.37); 8 (t = 0.18, df = 4.08, p = 0.87);
9 (t = 0.00, df = 15.55, p = 0.99); 10 (t = -1.22, df = 14.08, p = 0.24); 11 (t = -0.31, df = 15.99, p = 0.76); 12 (t = 0.42, df = 15.99, p = 0.68);
13 (t = -0.08, df = 8.42, p = 0.99); 14 (t = 1.41, df = 16.27, p = 0.17); 15 (t = 0.79, df = 6.65, p = 0.45); 16 (t = 0.93, df = 16.62, p = 0.36)

Table 3. Summary of results for covariates from multiple regression models evaluating felid interactions in relation to urbanization and space use for bobcats and pumas on the Western Slope (WS) and Front Range (FR) of Colorado. Covariates included Grid (sampling grid areas comparing urbanized (=0) and wildland grids (=1)), Space-Use Extent (extent of space use for animals), and Human Development (influence of human development at a kernel density radius of 1000m). Variable importance values (VIV) were calculated across model sets comprised of all possible combinations of covariates. Parameter estimates (β) and standard errors (se) were calculated by model averaging across all models in a model set in which the variable occurred.

Study Area	Comparison	Response Variable	Covariates: Grid VIF	Grid β (se)	Space-Use Extent VIF	Space-Use Extent β (se)	Human Development VIF	Human Development β (se)
WS	Bobcats with Pumas	Space-Use Overlap	0.20	0.01 (0.02)	0.95	0.02 (0.01)	0.25	0.01 (0.01)
WS	Bobcats with Pumas	Degree	0.27	-0.39 (0.39)	0.90	0.45 (0.16)	0.24	-0.18 (0.22)
WS	Bobcats with Pumas	In-strength	0.17	0.04 (0.09)	1.00	0.19 (0.04)	0.19	0.03 (0.05)
WS	Bobcats with Pumas	Equivalent Social Connectivity	0.99	17.76 (4.13)	1.00	46.51 (2.07)	0.15	-1.34 (3.04)
WS	Pumas with Bobcats	Space-Use Overlap	0.38	-0.07 (0.04)	0.26	-0.03 (0.02)	0.10	-0.01 (0.03)
WS	Pumas with Bobcats	Degree	0.11	3.07 (4.10)	0.41	3.12 (1.59)	0.15	2.12 (1.94)
WS	Pumas with Bobcats	In-strength	0.27	-0.63 (0.41)	0.20	-0.27 (0.20)	0.09	0.04 (0.24)
WS	Pumas with Bobcats	Equivalent Social Connectivity	0.04	13.18 (30.83)	1.00	59.36 (11.30)	0.80	30.44 (9.80)
FR	Bobcats with Pumas	Space-Use Overlap	0.17	0.00 (0.03)	0.45	0.02 (0.01)	0.19	0.01 (0.01)
FR	Bobcats with Pumas	Degree	0.24	-1.04 (1.06)	0.97	1.77 (0.53)	0.15	0.05 (0.58)
FR	Bobcats with Pumas	In-strength	0.16	-0.02 (0.37)	0.65	0.36 (0.17)	0.21	0.14 (0.19)
FR	Bobcats with Pumas	Equivalent Social Connectivity	0.34	29.91 (22.03)	1.00	48.25 (11.33)	0.15	1.63 (12.49)
FR	Pumas with Bobcats	Space-Use Overlap	0.17	0.00 (0.03)	0.70	-0.03 (0.01)	0.25	-0.01 (0.02)
FR	Pumas with Bobcats	Degree	0.33	2.39 (1.92)	0.82	2.25 (0.86)	0.26	1.09 (1.19)
FR	Pumas with Bobcats	In-strength	0.30	0.38 (0.35)	0.37	-0.23 (0.17)	0.20	-0.06 (0.20)
FR	Pumas with Bobcats	Equivalent Social Connectivity	0.19	10.49 (18.01)	1.00	65.80 (8.75)	0.17	3.38 (10.32)

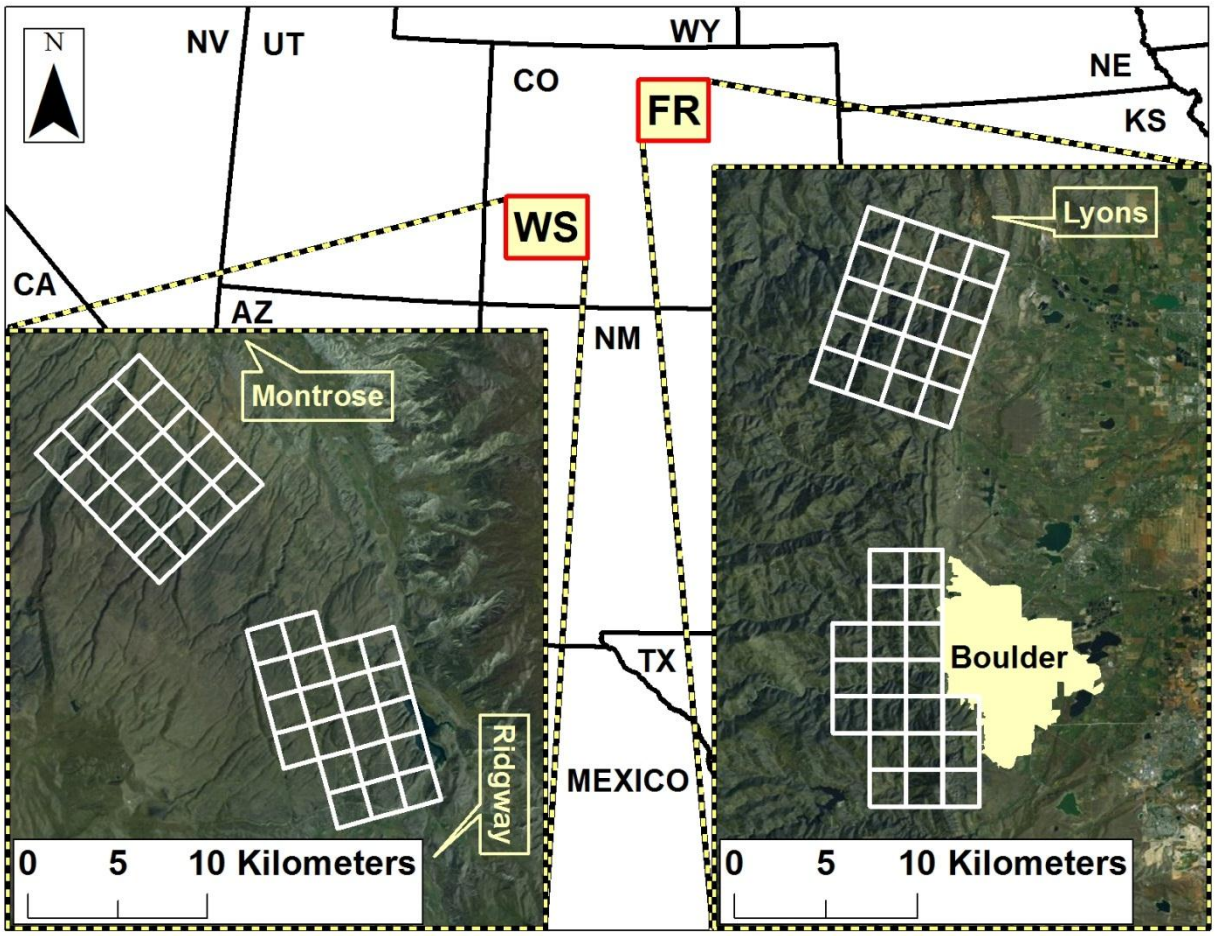


Figure 1. Locations of two study areas in Colorado, USA, which exhibited varying levels of urbanization, where bobcats and pumas were fit with telemetry collars. The more rural Western Slope (WS) was characterized by an exurban development south grid and a wildland north grid during 2009 – 2010. The more urbanized Front Range (FR) study area was characterized by a wildland-urban interface (WUI) south grid and wildland north grid during 2010 – 2012.

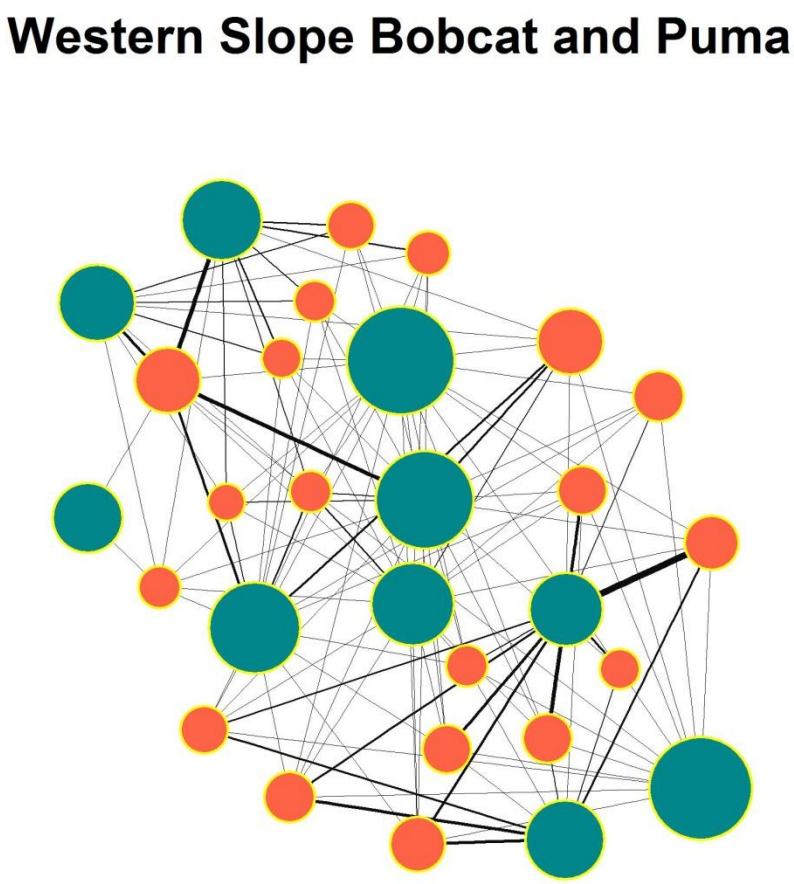


Figure 2a. WS contact network

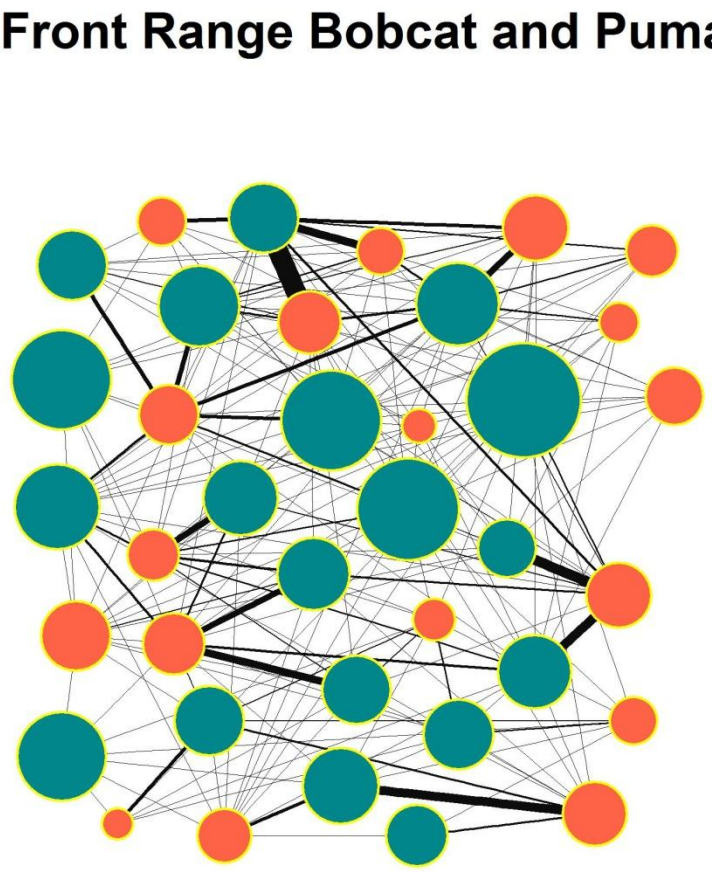


Figure 2b. FR contact network

Figure 2. Contact networks of interspecific interactions between bobcats and pumas on the Western Slope (WS) (a) and Front Range (FR) (b), Colorado, demonstrating *space-use overlap*, *degree*, and *in-strength*. Darker blue circles represent pumas and lighter red circles represent bobcats. Circle (i.e., node) size is proportional to space-use extent on the log scale. The thickness of edges between individuals increases with the amount of space-use overlap. Node

placement reflects approximate spatial location of individuals based on the center of their extent of space use; however, nodes were arranged to enhance visualization and do not reflect exact spatial orientation of individuals.

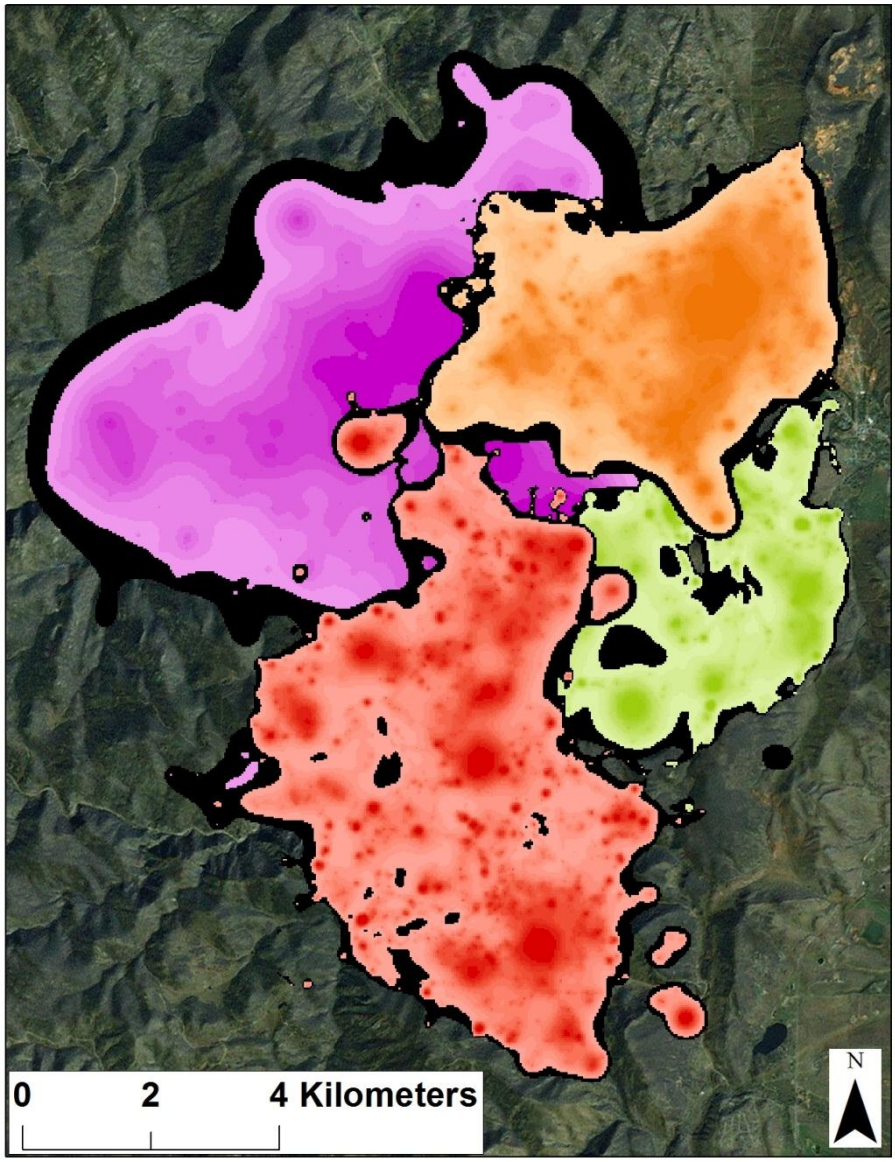


Figure 3a. Female puma (in purple) and 3 bobcats.

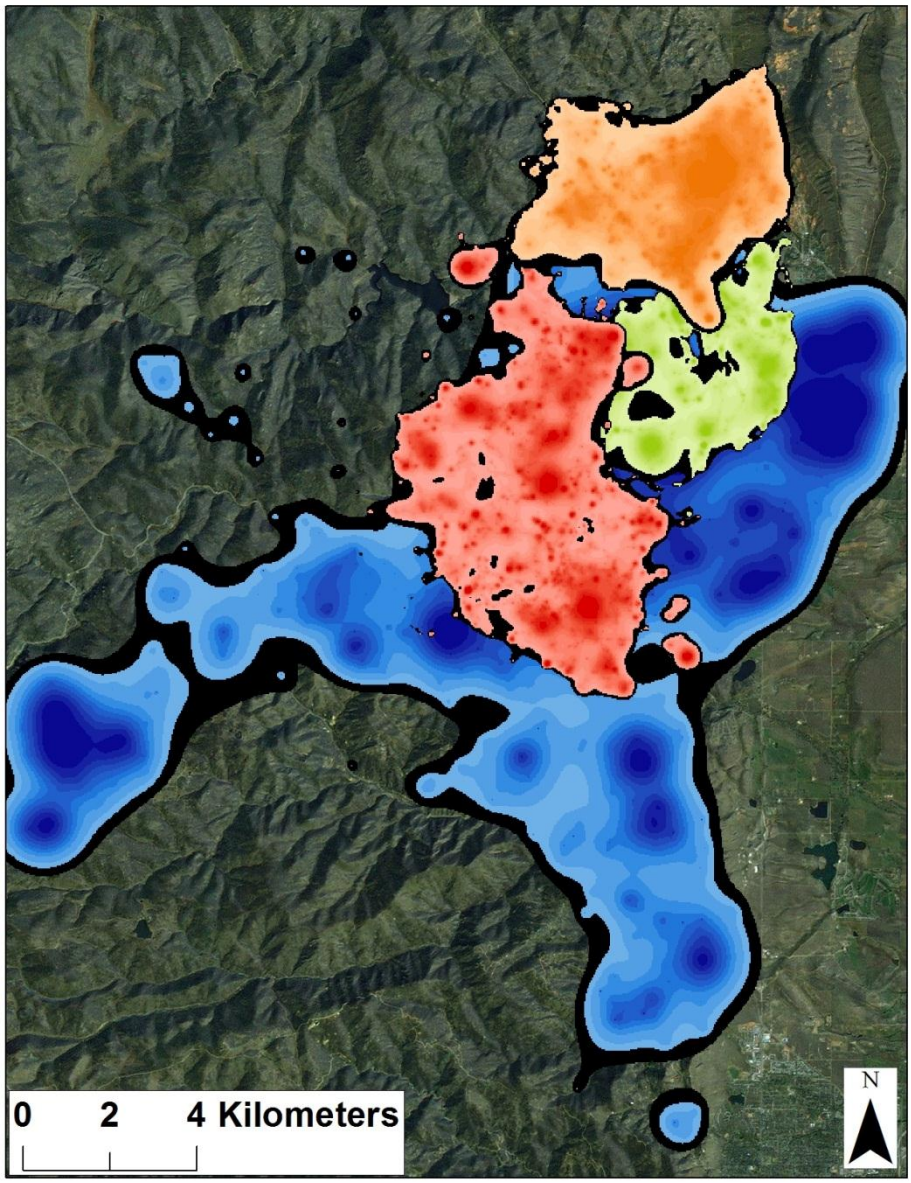


Figure 3b. Male puma (in blue) and 3 bobcats.

Figure 3. Example of space-use overlap between 3 bobcats and female (in purple) puma (a) and male (in blue) puma (b) on the Front Range, Colorado.

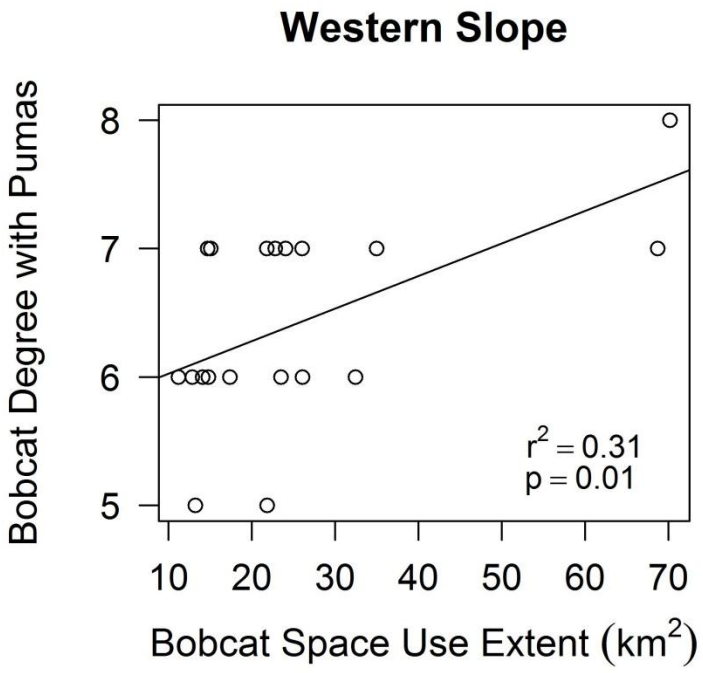


Figure 4a. Bobcats with pumas on WS

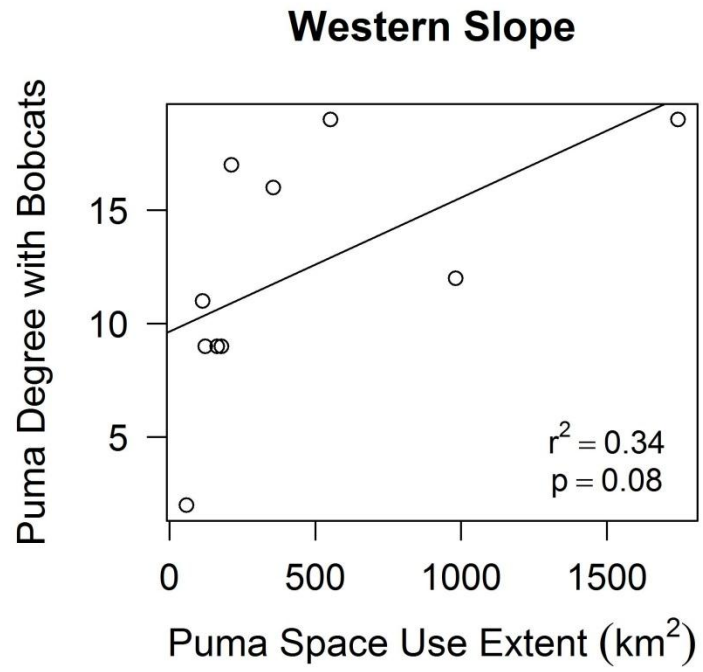


Figure 4b. Pumas with bobcats on WS

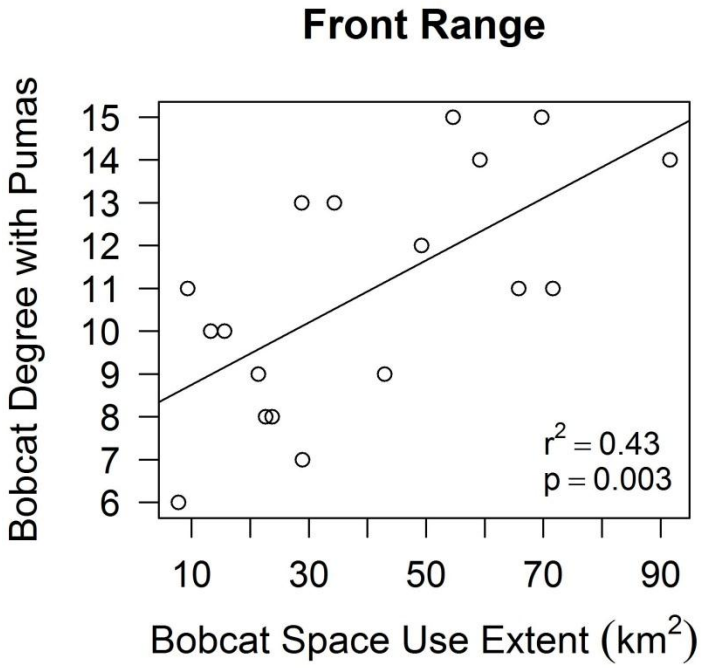


Figure 4c. Bobcats with pumas on FR

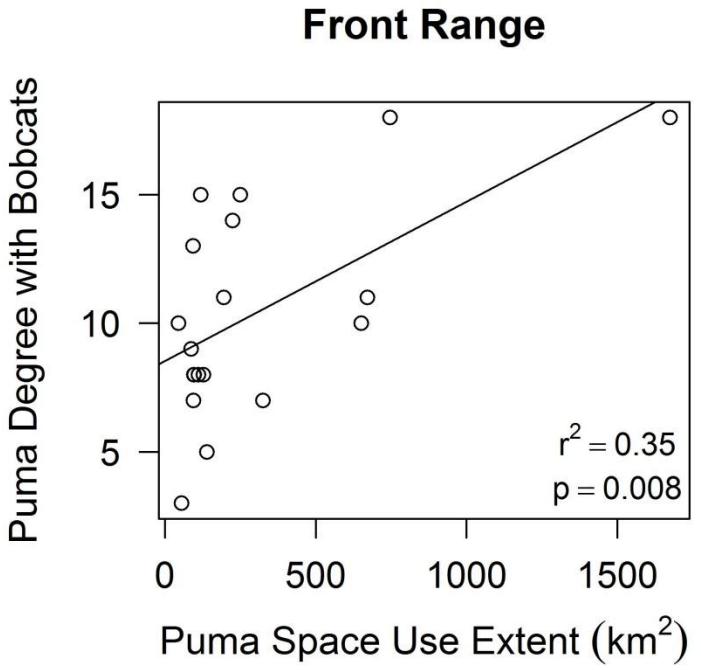


Figure 4d. Pumas with bobcats on FR

Figure 4. The number of potential interspecific interactions (i.e., *degree*) increased with the extent of space use for bobcats (a) and pumas (b) on the Western Slope and bobcats (c) and pumas (d) on the Front Range of Colorado. *Degree* is the number of individuals that overlapped in space use and thus had the potential to interact.

LITERATURE CITED

Adler, G. H., and R. Levins. 1994. The island syndrome in rodent populations. Quarterly Review of Biology:473-490.

Beier, P., S. P. D. Riley, and R. M. Sauvajot. 2010. Mountain lions (Puma concolor). Pages 141-155 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban carnivores: ecology, conflict and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Bradley, C. A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology & Evolution 22:95-102.

Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:1-21.

Burgman, M. A., and J. C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation 6:19-28.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition edition. Springer Verlag, New York, NY, USA.

Cohen, J. E. 2003. Human population: the next half century. Science 302:1172-1175.

Craft, M. E., and D. Caillaud. 2011. Network models: an underutilized tool in wildlife epidemiology? Interdisciplinary perspectives on infectious diseases 2011:1-12.

Crooks, K., S. Riley, S. Gehrt, T. Gosselink, and T. Van Deelen. 2010. Community ecology of urban carnivores. Pages 185-196 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban carnivores: ecology, conflict, and conservation. The John Hopkins University Press, Baltimore, MD, USA.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488-502.

Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation. Cambridge University Press, New York.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. Journal of Mammalogy 56:177-198.

Csardi, G. 2014. igraph. R Core Development Team.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife--threats to biodiversity and human health. Science 287:443-449.

Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. The Journal of Wildlife Management 66:1235-1245.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399-407.

Ferguson, A. W., N. A. Currit, and F. W. Weckerly. 2009. Isometric scaling in home-range size of male and female bobcats (Lynx rufus). Canadian Journal of Zoology 87:1052-1060.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346-1359.
Forman, R. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.
Franklin, S., J. Troyer, J. Terwee, L. Lyren, W. Boyce, S. Riley, M. Roelke, K. Crooks, and S. Vandewoude. 2007. Frequent transmission of immunodeficiency viruses among bobcats and pumas. Journal of virology 81:10961-10969.
Gehrt, S. D., S. P. Riley, and B. L. Cypher. 2010. Urban carnivores: ecology, conflict, and conservation. John Hopkins University Press, Baltimore, MD, USA.
Godfrey, S. S. 2013. Networks and the ecology of parasite transmission: A framework for wildlife parasitology. International Journal for Parasitology: Parasites and Wildlife 2:235-245.
Godfrey, S. S., J. A. Moore, N. J. Nelson, and C. M. Bull. 2010. Social network structure and parasite infection patterns in a territorial reptile, the tuatara (Sphenodon punctatus). International journal for parasitology 40:1575-1585.
Hadidian, J., S. Prange, R. Rosatte, S. Riley, and S. Gehrt. 2010. Raccoons (Procyon lotor). Pages 35-47 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Hamede, R. K., J. Bashford, H. McCallum, and M. Jones. 2009. Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecology Letters 12:1147-1157.
Harveson, L. A., M. E. Tewes, N. J. Silvy, and J. Rutledge. 2000. Prey use by mountain lions in southern Texas. The Southwestern Naturalist 45:472-476.
Hass, C. C. 2009. Competition and coexistence in sympatric bobcats and pumas. Journal of Zoology 278:174-180.
Hijmans, R. J. 2014. raster. R Core Development Team.
Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641-648.
_____. 2009. Animal Space Use 1.3 <http://www.cnr.uidaho.edu/population_ecology/animal_space_use>.
Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges Ecology 88:2354-2363.
Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:1-42.
Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy 72:391-396.
Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. Ecology 50:587-607.
Kreeger, T. J., J. M. Arnemo, and J. P. Raath. 2002. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado.
Lewis, J. S., L. L. Bailey, S. Vandewoude, and K. R. Crooks. 2014a. Interspecific interactions between wild felids across a gradient of urbanization. In review.

Lewis, J. S., K. A. Logan, M. W. Alldredge, L. L. Bailey, S. VandeWoude, and K. R. Crooks. 2014b. Population density and occupancy of wild felids across a gradient of urbanization. Dissertation Chapter 1.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C.

Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105-117 *in* M. Hornocker, andS. Negri, editors. Cougar ecology and conservation University of Chicago Press, Chicago, Illinois.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton, NJ.

Magle, S. B., V. M. Hunt, M. Vernon, and K. R. Crooks. 2012. Urban wildlife research: past, present, and future. Biological Conservation 155:23-32.

Newman, M. E. 2003. The structure and function of complex networks. SIAM review 45:167-256.

Nickerson, C., R. Ebel, A. Borchers, and F. Carriazo. 2011. Major uses of land in the United States, 2007. United States Department of Agriculture, Economic Research Service.

R. Development Core Team 2014. R: a language and environment for statistical computing, Version 3.0.2. R Foundation for Statistical Computing. Vienna, Austria.

Riley, S., E. Boydston, K. Crooks, and L. Lyren. 2010. Bobcats (Lynx rufus). Pages 121-138 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.

Riley, S. P. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. Journal of Wildlife Management 70:1425-1435.

Riley, S. P., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566-576.

Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733-1741.

Robert, K., D. Garant, and F. Pelletier. 2012. Keep in touch: does spatial overlap correlate with contact rate frequency? The Journal of Wildlife Management 76:1670-1675.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, United Kingdom.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY.

Saura, S., C. Estreguil, C. Mouton, and M. Rodríguez-Freire. 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). Ecological Indicators 11:407-416.

Saura, S., and L. Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning 83:91-103.

Schauber, E. M., D. J. Storm, and C. K. Nielsen. 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. The Journal of Wildlife Management 71:155-163.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103-113.
Schneider, A., M. Friedl, and D. Potere. 2009. A new map of global urban extent from MODIS satellite data. Environmental Research Letters 4:1-11.
Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. A meta-analysis of global urban land expansion. PLoS One 6:1-9.
Soulsbury, C., P. Baker, G. Iossa, and S. Harris. 2010. Red foxes (Vulpes vulpes). Pages 63-78 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. Johns Hopkins University Press, Baltimore, Maryland.
Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, IL, USA.
Terborgh, J., and J. A. Estes. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington D.C.
Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society 10:1-34.
Tracey, J. A. 2014. mkde. R Core Development Team.
Tracey, J. A., J. Zhu, E. Boydston, L. Lyren, R. N. Fisher, and K. R. Crooks. 2013. Mapping behavioral landscapes for animal movement: a finite mixture modeling approach. Ecological Applications 23:654-669.
Vander Wal, E., M. P. Laforge, and P. D. McLoughlin. 2014. Density dependence in social behaviour: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. Behavioral Ecology and Sociobiology 68:383-390.
Wey, T., D. T. Blumstein, W. Shen, and F. Jordán. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal Behaviour 75:333-344.
Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS One 8:e60590.

Appendix Table 1. Ranking of multiple regression models evaluating *space-use overlap* for bobcats with pumas on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	-74.37	0.00	0.60	40.99
7	SpaceUseExtent + HumDev	4	-71.82	2.55	0.17	41.34
5	Grid + SpaceUseExtent	4	-71.25	3.13	0.13	41.05
8	Grid + SpaceUseExtent + HumDev	5	-69.52	4.86	0.05	42.07
1	Intercept-only	2	-67.20	7.17	0.02	35.97
6	Grid + HumDev	4	-67.14	7.23	0.02	39.00
4	HumDev	3	-66.70	7.68	0.01	37.15
2	Grid	3	-64.67	9.70	0.00	36.14

Appendix Table 2. Ranking of multiple regression models evaluating *degree* for bobcats with pumas on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	43.53	0.00	0.52	-17.96
5	Grid + SpaceUseExtent	4	45.98	2.45	0.15	-17.56
7	SpaceUseExtent + HumDev	4	46.35	2.82	0.13	-17.74
8	Grid + SpaceUseExtent + HumDev	5	46.87	3.35	0.10	-16.13
1	Intercept-only	2	47.64	4.11	0.07	-21.44
2	Grid	3	50.25	6.73	0.02	-21.33
4	HumDev	3	50.43	6.90	0.02	-21.41
6	Grid + HumDev	4	53.51	9.98	0.00	-21.32

Appendix Table 3. Ranking of multiple regression models evaluating *in-strength* for bobcats with pumas on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	-6.23	0.00	0.67	6.92
7	SpaceUseExtent + HumDev	4	-3.25	2.98	0.15	7.05
5	Grid + SpaceUseExtent	4	-3.08	3.16	0.14	6.97
8	Grid + SpaceUseExtent + HumDev	5	-0.24	5.99	0.03	7.43
1	Intercept-only	2	6.37	12.60	0.00	-0.81
4	HumDev	3	7.28	13.51	0.00	0.16
6	Grid + HumDev	4	7.41	13.64	0.00	1.72
2	Grid	3	8.91	15.14	0.00	-0.66

Appendix Table 4. Ranking of multiple regression models evaluating *equivalent social connectivity* for bobcats with pumas on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
5	Grid + SpaceUseExtent	4	142.51	0.00	0.85	-65.82
8	Grid + SpaceUseExtent + HumDev	5	146.08	3.57	0.14	-65.73
7	SpaceUseExtent + HumDev	4	152.19	9.69	0.01	-70.67
3	SpaceUseExtent	3	155.31	12.80	0.00	-73.85
1	Intercept-only	2	205.46	62.95	0.00	-100.35
6	Grid + HumDev	4	205.89	63.39	0.00	-97.52
2	Grid	3	206.68	64.17	0.00	-99.54
4	HumDev	3	207.68	65.18	0.00	-100.04

Appendix Table 5. Ranking of multiple regression models evaluating *space-use overlap* for pumas with bobcats on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
1	Intercept-only	2	-22.73	0.00	0.39	14.22
2	Grid	3	-21.86	0.87	0.25	15.93
3	SpaceUseExtent	3	-21.11	1.62	0.17	15.55
5	Grid + SpaceUseExtent	4	-19.47	3.26	0.08	17.74
4	HumDev	3	-18.48	4.25	0.05	14.24
6	Grid + HumDev	4	-18.26	4.47	0.04	17.13
7	SpaceUseExtent + HumDev	4	-15.36	7.37	0.01	15.68
8	Grid + SpaceUseExtent + HumDev	5	-11.25	11.48	0.00	18.12

Appendix Table 6. Ranking of multiple regression models evaluating *degree* for pumas with bobcats on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
1	Intercept-only	2	66.91	0.00	0.40	-30.60
3	SpaceUseExtent	3	67.11	0.20	0.37	-28.55
4	HumDev	3	69.64	2.74	0.10	-29.82
2	Grid	3	70.75	3.85	0.06	-30.38
5	Grid + SpaceUseExtent	4	72.57	5.67	0.02	-28.29
7	SpaceUseExtent + HumDev	4	72.68	5.77	0.02	-28.34
6	Grid + HumDev	4	72.74	5.83	0.02	-28.37
8	Grid + SpaceUseExtent + HumDev	5	79.66	12.75	0.00	-27.33

Appendix Table 7. Ranking of multiple regression models evaluating *in-strength* for pumas with bobcats on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
1	Intercept-only	2	23.87	0.00	0.51	-9.08
2	Grid	3	25.55	1.67	0.22	-7.77
3	SpaceUseExtent	3	26.26	2.39	0.15	-8.13
4	HumDev	3	28.10	4.22	0.06	-9.05
5	Grid + SpaceUseExtent	4	29.24	5.37	0.03	-6.62
6	Grid + HumDev	4	31.06	7.19	0.01	-7.53
7	SpaceUseExtent + HumDev	4	31.40	7.52	0.01	-7.70
8	Grid + SpaceUseExtent + HumDev	5	38.24	14.37	0.00	-6.62

Appendix Table 8. Ranking of multiple regression models evaluating *equivalent social connectivity* for pumas with bobcats on the Western Slope of Colorado. Covariates included Grid (sampling areas comparing exurban development and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
7	SpaceUseExtent + HumDev	4	106.24	0.00	0.78	-45.12
3	SpaceUseExtent	3	109.12	2.88	0.18	-49.56
8	Grid + SpaceUseExtent + HumDev	5	113.10	6.86	0.03	-44.05
5	Grid + SpaceUseExtent	4	114.69	8.45	0.01	-49.34
4	HumDev	3	118.39	12.15	0.00	-54.19
1	Intercept-only	2	120.12	13.88	0.00	-57.20
6	Grid + HumDev	4	122.24	16.00	0.00	-53.12
2	Grid	3	124.37	18.13	0.00	-57.18

Appendix Table 9. Ranking of multiple regression models evaluating *space-use overlap* for bobcats with pumas on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
1	Intercept-only	2	-50.66	0.00	0.35	27.73
3	SpaceUseExtent	3	-50.43	0.23	0.32	29.07
4	HumDev	3	-48.10	2.56	0.10	27.91
2	Grid	3	-47.75	2.91	0.08	27.73
5	Grid + SpaceUseExtent	4	-47.15	3.51	0.06	29.11
7	SpaceUseExtent + HumDev	4	-47.15	3.51	0.06	29.11
6	Grid + HumDev	4	-44.81	5.85	0.02	27.94
8	Grid + SpaceUseExtent + HumDev	5	-43.41	7.25	0.01	29.21

Appendix Table 10. Ranking of multiple regression models evaluating *degree* for bobcats with pumas on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	84.02	0.00	0.62	-38.15
5	Grid + SpaceUseExtent	4	86.26	2.23	0.20	-37.59
7	SpaceUseExtent + HumDev	4	87.36	3.34	0.12	-38.14
8	Grid + SpaceUseExtent + HumDev	5	90.11	6.08	0.03	-37.55
1	Intercept-only	2	91.16	7.14	0.02	-43.18
2	Grid	3	92.47	8.45	0.01	-42.38
4	HumDev	3	93.58	9.55	0.01	-42.93
6	Grid + HumDev	4	95.78	11.76	0.00	-42.35

Appendix Table 11. Ranking of multiple regression models evaluating *in-strength* for bobcats with pumas on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	43.73	0.00	0.45	-18.01
1	Intercept-only	2	45.28	1.55	0.21	-20.24
7	SpaceUseExtent+ HumDev	4	46.65	2.92	0.10	-17.78
5	Grid+ SpaceUseExtent	4	47.09	3.36	0.08	-18.01
4	HumDev	3	47.18	3.45	0.08	-19.73
2	Grid	3	48.09	4.36	0.05	-20.19
8	Grid+ SpaceUseExtent+ HumDev	5	50.49	6.76	0.02	-17.75
6	Grid+ HumDev	4	50.54	6.81	0.01	-19.73

Appendix Table 12. Ranking of multiple regression models evaluating *equivalent social connectivity* for bobcats with pumas on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	194.76	0.00	0.55	-93.52
5	Grid + SpaceUseExtent	4	196.03	1.27	0.29	-92.48
7	SpaceUseExtent + HumDev	4	198.12	3.36	0.10	-93.52
8	Grid + SpaceUseExtent + HumDev	5	199.65	4.89	0.05	-92.32
1	Intercept-only	2	205.32	10.56	0.00	-100.26
4	HumDev	3	207.85	13.09	0.00	-100.07
2	Grid	3	208.03	13.28	0.00	-100.16
6	Grid + HumDev	4	210.62	15.86	0.00	-99.77

Appendix Table 13. Ranking of multiple regression models evaluating *space-use overlap* for pumas with bobcats on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	-51.02	0.00	0.48	29.31
1	Intercept-only	2	-48.55	2.47	0.14	26.65
7	SpaceUseExtent + HumDev	4	-48.01	3.01	0.11	29.43
4	HumDev	3	-47.92	3.10	0.10	27.76
5	Grid + SpaceUseExtent	4	-47.91	3.11	0.10	29.38
2	Grid	3	-45.70	5.32	0.03	26.65
6	Grid + HumDev	4	-44.96	6.06	0.02	27.91
8	Grid + SpaceUseExtent + HumDev	5	-44.28	6.74	0.02	29.45

Appendix Table 14. Ranking of multiple regression models evaluating *degree* for pumas with bobcats on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	106.16	0.00	0.49	-49.28
5	Grid + SpaceUseExtent	4	108.10	1.94	0.18	-48.62
7	SpaceUseExtent + HumDev	4	109.28	3.12	0.10	-49.21
6	Grid + HumDev	4	109.98	3.82	0.07	-49.56
8	Grid + SpaceUseExtent + HumDev	5	110.68	4.52	0.05	-48.03
1	Intercept-only	2	110.98	4.82	0.04	-53.11
4	HumDev	3	111.38	5.22	0.04	-51.89
2	Grid	3	112.07	5.91	0.03	-52.23

Appendix Table 15. Ranking of multiple regression models evaluating *in-strength* for pumas with bobcats on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
1	Intercept-only	2	44.74	0.00	0.35	-20.00
3	SpaceUseExtent	3	45.75	1.01	0.21	-19.07
2	Grid	3	46.48	1.74	0.14	-19.44
4	HumDev	3	47.08	2.33	0.11	-19.74
5	Grid + SpaceUseExtent	4	47.19	2.45	0.10	-18.17
7	SpaceUseExtent + HumDev	4	49.00	4.26	0.04	-19.07
6	Grid + HumDev	4	49.58	4.84	0.03	-19.36
8	Grid + SpaceUseExtent + HumDev	5	50.49	5.75	0.02	-17.94

Appendix Table 16. Ranking of multiple regression models evaluating *equivalent social connectivity* for pumas with bobcats on the Front Range of Colorado. Covariates included Grid (sampling areas comparing wildland-urban interface and wildland grids), SpaceUseExtent (extent of space use for animals), and HumDev (influence of human development at a kernel density radius of 1000m). (.) denotes intercept only model.

#	Covariates	K	AICc	Δ AICc	ω	LL
3	SpaceUseExtent	3	194.96	0.00	0.67	-93.68
5	Grid + SpaceUseExtent	4	197.86	2.90	0.16	-93.50
7	SpaceUseExtent + HumDev	4	198.14	3.17	0.14	-93.64
8	Grid + SpaceUseExtent + HumDev	5	201.18	6.22	0.03	-93.28
6	Grid + HumDev	4	219.13	24.17	0.00	-104.14
4	HumDev	3	219.65	24.69	0.00	-106.03
1	Intercept-only	2	221.52	26.56	0.00	-108.39
2	Grid	3	223.61	28.65	0.00	-108.01

THE EFFECTS OF DEMOGRAPHIC, SOCIAL, AND ENVIRONMENTAL CHARACTERISTICS ON PATHOGEN EXPOSURE IN WILD FELIDS ACROSS A GRADIENT OF URBANIZATION [4]

OVERVIEW

Transmission of pathogens among animals is influenced by demographic, social, and environmental factors. Through altering landscape pattern, particularly from urbanization, humans can impact patterns of disease dynamics in wildlife populations, increasing the potential for the spillover and spread of emerging infectious diseases in wildlife, human, and domestic animal populations. We provide a conceptual framework for evaluating the effects of multiple ecological mechanisms on patterns of pathogen exposure in animal populations. Specifically, we evaluated how ecological factors affected the prevalence of *Toxoplasma gondii* (Toxoplasma), *Bartonella spp.* (Bartonella), feline immunodeficiency virus (FIV), and feline calicivirus (FCV) in bobcat and puma populations across low-density exurban development, wildland-urban interface (WUI), and wildland habitat on the Western Slope (WS) and Front Range (FR) of Colorado. As predicted, age appeared to be positively related to the exposure to pathogens that are both environmentally transmitted (Toxoplasma) and directly transmitted between animals (FIV). In addition, animals (WS bobcats) were more likely to be exposed to a pathogen acquired from prey and the environment (Toxoplasma) with increasing age and intraspecific space-use overlap. However, counter to our predictions, exposure to directly-transmitted pathogens (FCV and FIV) for felids was more likely with decreasing space-use overlap (FCV: WS bobcats) and potential intraspecific contacts (FIV: FR pumas), potentially related to whether animals were

[4] Jesse S. Lewis, Kenneth A. Logan, Mat W. Alldredge, Scott Carver, Sarah N. Bevins, Michael Lappin, Sue VandeWoude, Kevin R. Crooks

residents or transients. In addition, consistent with predictions, bobcats that used similar habitat areas as pumas exhibited increased exposure to Bartonella. Counter to our predictions, environmental factors, including urbanization and landscape covariates, were generally unsupported in our models. We demonstrated how pathogens can be evaluated in relation to demographic, social, and environmental factors to understand pathogen exposure in animal populations; such a framework is useful because it allows for the comparison and evaluation of the relative strength among multiple mechanisms and hypotheses.

INTRODUCTION

Infectious diseases play important roles in wildlife conservation and are implicated in threatening species and populations across local to global scales (Murray et al. 1999, Czech et al. 2000, Daszak et al. 2000, Pedersen et al. 2007, Dybas 2009, Seimon et al. 2013). Through landscape modification and altering of wildlife communities, humans can influence patterns of disease dynamics in wildlife populations (Morse 1995, Daszak et al. 2000, Levi et al. 2012, Young et al. 2014), increasing the potential for the spillover and spread of emerging infectious diseases in wildlife, human, and domestic animal populations (Daszak et al. 2000, McMichael 2004, Woolhouse et al. 2005, Keesing et al. 2010). In particular, urbanization is a major driver in altering landscape pattern. The conversion of undeveloped land to human development, including residences, buildings, and roads, is one of the most extensive anthropogenic disturbances affecting wildlife populations around the world (Sala et al. 2000, McDonald et al. 2008) and urbanization is projected to increase by millions of hectares over the next few decades (Cohen 2003, Theobald 2005, Seto et al. 2011). To conserve animal populations and reduce the risk of infectious and zoonotic pathogens in wildlife and humans, it is critical to understand the

mechanisms that alter patterns of disease in wildlife populations across different forms of urbanization, particularly as it relates to modes of pathogen transmission (Daszak et al. 2001, Shochat et al. 2006, Bradley and Altizer 2007, Bradley et al. 2008).

Transmission of pathogens among animals is influenced by demographic, social, and environmental factors (Morse 1995, Altizer et al. 2003b, Wilcox and Gubler 2005), as well as through pathogen characteristics and host susceptibility (Altizer et al. 2003a). With regard to demography, males and older individuals often exhibit a greater prevalence of parasites and disease (Hudson and Dobson 1995, Zuk and McKean 1996, Wilson et al. 2002, Biek et al. 2006b, Monello and Gompper 2009). Males tend to have larger extents of space use (Lindstedt et al. 1986) and greater potential for contacts among animals (Lewis et al. 2014b). Some animals in a population might be more likely than others to spread disease based on demographic and individual characteristics (Woolhouse et al. 1997, Paull et al. 2012). In addition, increases in population density can result in higher contact rates (Ramsey et al. 2002) and greater prevalence and diversity of pathogens among highly connected individuals (Altizer et al. 2003b). However, in contrast, transmission of parasites within populations can decrease with increasing host density, potentially due to host behavior, such as less mixing among individuals within a population, which leads to more localized disease transmission (Fenton et al. 2002).

Social organization plays an important role in disease transmission through intra- and interspecific interactions and contact patterns (Altizer et al. 2003b, Tompkins et al. 2011). For many solitary species (such as many carnivores), intraspecific social interactions primarily occur during the mating season or when defending and maintaining territorial boundaries (Sunquist and Sunquist 2002). In addition, space-use overlap of animals can lead to kleptoparasitism (where one animal steals the food of another; Gorman et al. 1998, Merkle et al. 2009), aggressive

encounters, and intraguild predation (Polis et al. 1989, Palomares and Caro 1999), which can increase the opportunity for transmission of pathogens through direct and indirect interactions (Totton et al. 2002, Dybas 2009). Interspecific interactions can be important determinants of pathogen spillover from a reservoir species to another species, which can result in population decline and extirpation (Rushton et al. 2000, Gurnell et al. 2006, Dybas 2009). Although social organization is often associated with direct contacts between animals, overlap in space use and maintaining territorial boundaries through marking behavior can also influence indirect pathways of disease transmission for animals using shared areas through environmental transmission of pathogens (Afonso et al. 2008).

Lastly, the environment plays a critical role in disease transmission. Landscape characteristics, including habitat features, geographic barriers, and anthropogenic factors, can influence the spread and occurrence of pathogens (Smith et al. 2002, Russell et al. 2004, Biek et al. 2006a, McCallum 2008, Wheeler et al. 2010) and land-use change can have important implications for the distribution and abundance of pathogens (Vanwambeke et al. 2007a). Urbanization can alter the environmental conditions that influence the transmission and prevalence of pathogens through modifying landscape pattern (Langlois et al. 2001, Farnsworth et al. 2005, Skelly et al. 2006, Bradley and Altizer 2007, Brearley et al. 2013) and disease spillover (Gilot-Fromont et al. 2012). Several pathogens originating from anthropogenic sources can increase in prevalence in animal populations associated with urbanized environments (Carver et al. 2012). In some systems, environmental characteristics appear to be a more important factor in disease exposure than social or demographic factors. Although population densities for some species can be substantially higher in urban environments compared to rural areas, the number of infected individuals and burden of disease vectors can be substantially

greater in rural populations as a result of the population ecology of intermediate hosts for pathogens (Hegglin et al. 2007, Reperant et al. 2007, Page et al. 2008, Reperant et al. 2009). Agricultural areas can experience high prevalence of Toxoplasma due to abundant small mammals acting as intermediate hosts (Lélu et al. 2010).

Carnivores harbor a suite of pathogens, which can impact predator populations, ecological communities, and human health (Murray et al. 1999). Bobcats (*Lynx rufus*) and pumas (*Puma concolor*), which share a broad geographic distribution in western North America, demonstrate patterns and prevalence of pathogens in relation to anthropogenic factors (Wheeler et al. 2010, Bevins et al. 2012). Cross-species transmission of species-specific pathogens has been reported between bobcats and pumas in highly urbanized landscapes, potentially as a result of increased contacts and aggressive encounters resulting from elevated space-use overlap within habitat fragments (Franklin et al. 2007). Domestic cats (both feral and owned) are associated with human residences and harbor a suite of pathogens that can be transmitted to or from wild felids in rural and urbanized environments (Breitschwerdt and Kordick 2000, Deplazes et al. 2011, Bevins et al. 2012, Gilot-Fromont et al. 2012). Thus, bobcats and pumas are excellent model species to evaluate the effects of demographic, social, and environmental characteristics on patterns of pathogens within and between their populations.

Our goal here was to investigate how multiple mechanisms influence exposure to a suite of pathogens in medium and large-sized carnivores persisting across a gradient of urbanization. We evaluated bobcat and puma populations across low-density exurban development, wildland-urban interface (WUI), and wildland habitat in relation to four common pathogens in felids: *Toxoplasma gondii* (Toxoplasma), *Bartonella spp.*(Bartonella), feline immunodeficiency virus (FIV), and feline calicivirus (FCV). We predicted that (1) pathogens acquired primarily through

prey and the environment (i.e., Toxoplasma) would be associated with suitable habitat for the pathogen and greater amounts of space use sharing among felids; (2) pathogens transmitted by flea vectors (i.e., Bartonella) would be associated with habitat that harbored fleas and increased social interactions (i.e., space-use overlap and number of potential contacts); and (3) pathogens that are directly transmitted between individuals (i.e., FIV and FCV) would be positively related to social interactions (Table 1). In addition, owing to potential associations with domestic cats, we expected that animals associated with habitat modified by urbanization (exurban and WUI) would exhibit greater prevalence of each pathogen compared to wild felids within wildland areas (Table 1). Consistent with previous research, we also expected that older individuals and males would be more likely to be exposed to pathogens (Bevins et al. 2012). We present a framework for evaluating how pathogens in animal populations are influenced by demographic, social interaction (both intra- and interspecific), and environmental characteristics.

STUDY AREA

We conducted our research across two study areas in Colorado, USA that exhibited varying degrees of urbanization and human influence. In 2009-2010, we worked on the Western Slope (WS) of Colorado on the Uncompahgre Plateau near the towns of Montrose and Ridgway (Figure 1). Common vegetation included pinyon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), gambel oak (*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). We divided the WS study site into two sampling grids. The southern grid 1 sampled low-density residential development on Log Hill Mesa (population = 1,041; US Census Bureau 2010); residential parcel sizes were distributed, from most to least numerous, across 5 acre, 2 acre, 1 acre, ≥ 5 acre, and ≥ 40 acre

properties. Within areas of exurban development, travel corridors of natural habitat and open space property, often with associated recreation trails, were present. In addition, domestic cats (free-ranging owned and feral cats) occurred on grid 1. The northern grid 2 sampled primarily undeveloped, wildland habitat, although some small areas of low-density human residences and hunting camps occurred on or near the grid. Although less common compared to grid 1, a small number of domestic cats also occurred on grid 2.

In 2010 - 2012, we worked on the more urbanized Front Range (FR) of Colorado (Figure 1). Common vegetation included ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), juniper, aspen, and mountain mahogany (*Cercocarpus montanus*). A network of open space properties with recreational trails occurred across the study area. Similar to the WS, we divided the FR study area into two sampling grids. The southern grid 1 occurred adjacent to the wildland-urban interface (WUI) associated with the city of Boulder (population = 97,385, US Census Bureau 2010) and was characterized by open-space properties with some human residences on or near the grid. The northern grid 2 occurred across undeveloped public properties, although a small number of rural human residences occurred on private property inholdings. Domestic cats occurred across portions of both grids 1 and 2, but were assumed to be more common along the WUI with Boulder compared to the wildland grid. In addition, to the east of both sampling grids, and surrounding the city of Boulder, grasslands and agricultural areas interspersed with human residences occurred. See Lewis et al. (2014c) for an expanded description of the study area.

METHODS

Animal Capture and Telemetry Data

Bobcats were captured in black metal-wire cage traps (40 x 55 x 100 cm) with attractants from mid-June through March 2009 – 2011. All cage traps were fit with very high frequency (VHF) trap transmitters (Telonics Inc., Mesa, AZ, USA) that indicated when trap doors closed. Captured bobcats were immobilized through hand-injection of a combination of Ketamine (10.0 mg/kg) and Xylazine (1.0 mg/km), and Yohimbine (0.125 mg/km) was used to reverse Xylazine (Kreeger et al. 2002). We fit GPS collars (210 – 280 g, Telemetry Solutions, Concord, CA, USA) with timed drop-off mechanisms and degradable cotton spacers along the collar belting on adult-sized bobcats. GPS collars were programmed to record locations on the WS every 5-7 hours and on the FR every 3-4 hours. GPS collars were also equipped with VHF beacons that lasted up to 2 years, which allowed for the continued monitoring of animals to assess site fidelity to an area. Bobcats were weighed, sex was recorded, and age was estimated based on tooth development (Crowe 1975), wear, and coloration. Pumas were captured from 2005 – 2011 with the use of hounds and baited cage traps, immobilized with Telazol (5.0 – 9.0 mg/kg), and fit with GPS collars (Lotek, Newmarket, Ontario, Canada; Northstar, King George, VA, USA; Vectronics, Berlin, Germany) programmed to record a location every 5-7 hours on the WS and 3-4 hours on the FR. To increase the duration of time that location data were acquired for pumas on the WS, some individuals were fit with VHF collars (Lotek) and aerial positional locations were obtained approximately every 2 weeks. Pumas were also weighed, fit with eartags, and age and sex were recorded. Methods for animal capture were approved by the Colorado State University Animal Care and Use Committee (11-2453A).

Screening of Pathogens in Felids

For each captured bobcat and puma, we collected blood (~10 mL), tissue, hair, saliva, scat, and ectoparasite (tick, flea) samples from immobilized animals for pathogen analysis. Serum samples were analyzed for antibodies of Toxoplasma (enzyme-linked immunosorbent assay; ELISA), Bartonella (ELISA), FIV (Western Blot analysis), and FCV (ELISA) (Bevins et al. 2012). Based on serum sample evaluations, individuals were classified as testing positive (i.e., pathogen detected = 1) or negative (i.e., pathogen not detected = 0).

Pathogen Characteristics and Predictions

We hypothesized that multiple ecological factors would affect pathogen exposure in felid populations and focused our predictions on the expected relative strength that each mechanism would contribute to exposure of pathogens in felid populations (Table 1).

Toxoplasma gondii (Toxoplasma) is a common pathogen in felids, with seroprevalence ranging from approximately 20 - 90% (Franti et al. 1976, Paul-Murphy et al. 1994, Kikuchi et al. 2004, Riley et al. 2004, Bevins et al. 2012). Felids (domestic and wild cats) are the definitive host of Toxoplasma, in that infected animals excrete millions of oocysts into the environment over a period of several weeks. Resistant oocysts can survive for months and up to one year (Dubey 2010, Lélu et al. 2010). Felids can become infected by consuming infected prey, or less commonly, through direct environmental contamination by ingesting oocysts (Gilot-Fromont et al. 2012). Once the infection is cleared, felids are assumed to be immune to reinfection and cease shedding oocysts into the environment (Dubey 2010, Lélu et al. 2010). Although Toxoplasma generally does not cause fitness effects in felids or humans, there are known behavioral impacts, and individuals that have a weakened immune system can experience complications (Dubey 2010, Flegr 2013). Environment and prey characteristics dictate patterns

of Toxoplasma across the landscape (Table 1). Toxoplasma is associated with domestic cats, and thus can be more prevalent near areas of human residences, although the prevalence of Toxoplasma is predicted to vary across different forms or urbanization (Lélu et al. 2010). Low density urbanization, such as agricultural areas, can experience especially high prevalence of Toxoplasma due to an abundance of small mammals acting as intermediate hosts and sufficient predation of infected prey by domestic and wild felids. Urban areas are predicted to exhibit lower prevalence of Toxoplasma due to fewer intermediate hosts and reduced numbers of predation events (Lélu et al. 2010, Gilot-Fromont et al. 2012, Afonso et al. 2013, Gotteland et al. 2014). Toxoplasma is reported to be more prevalent, and oocysts survival might be extended, in cool and wet years and locations across regional to local areas (Afonso et al. 2010, Gilot-Fromont et al. 2012, Afonso et al. 2013). Based on these relationships, we expect that animals with greater amounts of the landscape characterized by moist conditions (i.e., Normalized difference vegetation index; NDVI; Table 2) present in their extent of space use would have a greater opportunity to be exposed to Toxoplasma (Table 1).

Bartonella spp. (Bartonella) are a bacteria transmitted through flea, tick, and other arthropod vectors and can possibly lead to persistent or recurrent infection (Breitschwerdt and Kordick 2000). The bacteria are not generally deleterious to felid health, but can cause "cat scratch disease" in humans. The prevalence of Bartonella is generally moderate in bobcat (approximately 15 – 75%) and low in puma (approximately 10 – 40%) populations (Chomel et al. 2004, Riley et al. 2004, Bevins et al. 2012), where prevalence likely reflects each species' exposure to arthropod vectors (Breitschwerdt and Kordick 2000, Bevins et al. 2012). Similar to Toxoplasma, Bartonella is associated with domestic cats (Table 1), which can potentially transmit the pathogen to wild felids primarily through flea vectors (Breitschwerdt and Kordick

2000). Bartonella is more prevalent in warm and humid climates where flea survival is increased (Yamamoto et al. 1998, Chomel et al. 2006) and ticks can be associated with more moist environments (Hugh-Jones et al. 1992, Estrada-Peña 2001, Estrada-Peña 2002). Therefore, we might also expect that on finer spatial scales, animals with greater amounts of the landscape characterized by mesic environments (e.g., as measured by NDVI) within their extents of space use would have a greater likelihood of being exposed to vectors that harbor Bartonella (Table 1).

Feline immunodeficiency virus (FIV) is the felid equivalent of human immunodeficiency virus (HIV) and typically occurs at moderate levels in bobcat and puma populations (approximately 20 – 60% prevalence) (Roelke et al. 1993, Biek et al. 2006b, Franklin et al. 2007, Bevins et al. 2012); however, it reportedly is not detected (prevalence of 0% for bobcats) in some populations (Riley et al. 2004, Lagana et al. 2013). Each felid species is typically infected with a unique strain of FIV (Troyer et al. 2005, VandeWoude and Apetrei 2006). Although transmission events of FIV primarily occur through direct intraspecific interactions (contacts within species; e.g., fighting or mating), direct interspecific interactions (contacts between species; e.g., aggressive encounters or intraguild predation) can also result in FIV transmission. Such transmission events, however, are likely uncommon in nature (VandeWoude and Apetrei 2006, Franklin et al. 2007, Troyer et al. 2008, Lagana et al. 2013). Felids are infected with FIV throughout their lifetime; although it is believed that most felids don't demonstrate clinical signs of infection, some individuals can potentially exhibit complications after many years of infection (Troyer et al. 2005, Pecon-Slattery et al. 2008). Because FIV is transmitted through direct contacts, greater prevalence is expected in populations that exhibit more opportunity for interactions (Table 1). For example, populations that occur at higher densities would be expected to result in greater prevalence of FIV (Troyer et al. 2005). Landscape pattern that is

altered through urbanization can potentially influence population density and animal movement patterns, which could increase intra- and interspecific interactions (Crooks et al. 2010) and thus the opportunity for FIV to be transmitted (Franklin et al. 2007, Tracey et al. 2014).

Feline calicivirus (FCV) is a widespread pathogen in felids, occurring at moderate levels in bobcat (prevalence ranging from 17 – 67%) (Riley et al. 2004) and puma (prevalence ranging from 17 – 56%) populations (Roelke et al. 1993, Paul-Murphy et al. 1994, Foley et al. 2013). Although highly infectious and easily transmitted through direct contacts between animals, it typically only causes minor to moderate oral, ocular, and upper respiratory disease; however, recently more virulent outbreaks have occurred in domestic cats resulting in high mortality (Radford et al. 2007). It is believed that felids can shed the virus for up to several months (and uncommonly throughout their lifetime) and although cats are believed to clear the virus, they can be reinfected with a related or novel viral variant of FCV (Radford et al. 2007). The prevalence of FCV increases with cat density (Radford et al. 2007), thus increased contacts among animals increase the likelihood of being infected (Table 1). Further, although FCV is probably most commonly transmitted via direct contacts between animals, the virus can persist in the environment (at least in clinical settings) for up to several weeks and thus potentially be transmitted indirectly (Radford et al. 2007), although it is unknown if this occurs in the natural environment. FCV can also be shed through urine and feces, although it is unknown if this is a potential source of environmental contamination and transmission (Radford et al. 2007). Because FCV is associated with domestic cats, the prevalence of the pathogen would be expected to increase with the proximity to human residences where owned and feral cats reside and interactions with wild felids are most likely to occur (Riley et al. 2004) (Table 1). Lastly,

within wild felid populations, the prevalence of FCV would be expected to follow similar predictions as presented for FIV above (Table 1).

Modeling Approach

Pathogen Prevalence for Felids Across Forms of Urbanization

For each grid and study area, we evaluated bobcat and puma exposure to pathogens. We estimated the seroprevalence of each pathogen within felid populations across exurban development and wildland habitat on the WS and WUI and wildland habitat on the FR.

Evaluation of Demographic, Social, and Environmental Factors

Based on our predictions of pathogen prevalence in bobcat and puma (Table 1), we compared a suite of models (Burnham and Anderson 2002, Plowright et al. 2008) evaluating demographic, social, and environmental characteristics for each pathogen in felid populations (Tables 2 and 3). Covariates were grouped into one of five categories: demographic, social intraspecific, social interspecific, environment urban, or environment landscape (Table 3). We defined social interactions as potential direct or indirect contacts occurring between animals, including both intra- and interspecific interactions. Although social behavior is most commonly associated with intraspecific interactions (e.g., Seidensticker et al. 1973, VanderWaal et al. 2014), social interactions can also occur between species, for example in the context of interspecific dominance relationships (Morse 1974, Farine et al. 2012).

Using logistic regression in R (i.e., glm with binomial logit link; R Development Core Team 2014), we evaluated model sets that were comprised of all possible combinations of univariate covariates and pairwise comparisons (56 total models) for each species in each study area and ranked models using Akaike's Information Criteria corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We evaluated all possible combinations of covariates in

models (Doherty et al. 2012) with up to 2 covariates based on sample size recommendations of evaluating 1 covariate per 5-10 observations (Hosmer et al. 2013). To evaluate the relative importance of variables in models, we calculated variable importance values (VIV) and model-averaged parameter estimates across models in which they occurred (Burnham and Anderson 2002). Likely due to either relatively low or high prevalence of the pathogen in logistic regression models, coupled with relatively low sample sizes, models sometimes failed to converge; these models generally had little support in our data sets (i.e., AIC weight ≤ 0.01). To calculate VIV and model-averaged parameter estimates for model sets in which some models failed to converge, these models were removed due to unusable values. To evaluate which covariates were supported in our model sets, we first identified covariates based on whether they occurred in models that performed better than the intercept-only model. For those covariates that appeared in top-ranked models, we then evaluated their VIV in model sets and the direction of their model-averaged parameter estimates. VIVs can be used to rank and compare the relative importance of covariates in model sets (Anderson 2008).

We used a variety of data sets and techniques to formulate demographic, social, and environmental covariates (Figure 2; Table 1). Telemetry data were used to estimate space use of individuals by calculating the utilization distribution (UD) for felids that occurred on our sampling grids from June 2009 to June 2010 on the WS and September 2010 to September 2011 on the FR (Lewis et al. 2014b). For animals fit with GPS collars (bobcats n = 37; pumas n = 25), UDs were estimated with the Brownian bridge movement model (BBMM) with the mkde package (Tracey 2014) in program R (R Development Core Team 2014). For pumas on the WS fit with VHF collars (n = 4), UDs were estimated with the kernel home range estimator using likelihood cross validation (Horne and Garton 2006) in the Animal Space Use package (Horne

and Garton 2009). We used the 99% cumulative probability of space use for all analyses. To evaluate the opportunity for direct and indirect contacts between individuals, we estimated *space-use overlap* among animals (Godfrey et al. 2010, Robert et al. 2012, Vander Wal et al. 2014); this information was used to estimate *degree*, *in-strength*, and *equivalent social connectivity* for intra- and interspecific social interactions (Table 1) (Lewis et al. 2014b). We also evaluated several environmental covariates, including the *amount of urbanization in space-use extent*, *grid*, and NDVI (Table 1). Each continuous covariate was standardized by subtracting the sample mean from the input variable values and dividing by the standard deviation (Schielzeth 2010). Covariates were evaluated for multi-collinearity using Pearson's correlation and considered correlated if $r > 0.7$; amount of NDVI in *space-use extent* and intra- and interspecific *in-strength* and *effective social connectivity* were highly correlated with multiple covariates for felid populations and these covariates were subsequently excluded from analyses. In addition, *space-use extent* for WS and FR pumas and *interspecific-degree* for FR pumas were highly correlated with multiple covariates and were excluded from analyses. For further explanations about how social interaction and urban covariates were calculated see Table 1 and Lewis et al. (2014b).

RESULTS

We sampled 37 bobcats and 29 pumas on the WS and FR during the course of our study. Both felids used areas in close proximity to human residences in exurban development and along the wildland-urban interface. Seroprevalence was evaluated for 71% - 100% of individuals within populations for specific pathogens (Figure 2), with the proportion of the sampled population screened based on sample quantity and quality. Although seroprevalence for some

pathogens varied between grids (Figure 2), we did not find support for a statistical difference in seroprevalance between urbanized and wildland grids based on the covariate Grid not occurring in top models (Appendix Tables 1-15) and not exhibiting support based on VIVs (Table 4) or model-averaged parameter estimates (Table 5).

Effects of Demographic, Social, and Environmental Factors

We evaluated 15 model sets to understand how demographic, social, and environmental factors influenced pathogen exposure in bobcats, although sample size restricted the number of models that we could evaluate in some instances (Appendix Tables 1 – 15).

Demographic Factors

As predicted for some pathogens, individuals were more likely to be exposed with increasing age; this covariate occurred in the top-ranked models for FIV in WS bobcats (Appendix Table 3) and Toxoplasma in FR bobcats (Appendix Table 9) and FR pumas (Appendix Table 12); VIV in these instances were relatively high ranging from 0.34 to 0.51 (Table 4), and the model-averaged parameter estimates indicated a positive trend between exposure and age (WS bobcats FIV: $\beta = 0.71$, se = 0.47; FR bobcats Toxoplasma: $\beta = 0.57$, se = 0.44; FR pumas Toxoplasma: $\beta = 1.08$, se = 0.69; Table 5). For *space-use extent*, counter to our predictions, there was a negative relationship with FCV for WS bobcats ($\beta = -1.72$, se = 1.24; Table 5); this covariate occurred in top-ranked models (Appendix Table 4) and had a VIV = 0.42 (Table 4). In support of our predictions, *space-use extent* for FIV in FR bobcats occurred in the top-ranked three models (Appendix Table 11) with a VIV = 0.55 (Table 4) and a positive relationship with exposure ($\beta = 2.54$, se = 2.34; Tables 5).

Social Factors

As predicted, WS bobcats appeared more likely to be exposed to Toxoplasma with increasing *intraspecific space-use overlap* ($\beta = 1.06$, se = 0.63; Table 5); this covariate occurred in the top-ranked model (Appendix Table 1) with a VIV = 0.41 (Tables 4). However, counter to predictions for directly transmitted pathogens, exposure to FCV for WS bobcats and FIV for FR pumas appeared negatively related to *intraspecific space-use overlap* ($\beta = -1.72$, se = 1.26) and *intraspecific degree* ($\beta = -4.05$, se = 2.79), respectively (Tables 5); these covariates occurred in the suite of top-ranked models (Appendix Tables 4 and 14, respectively) with VIVs of 0.55 and 0.84, respectively (Table 4). Interestingly, there appeared to be a positive relationship of exposure to Bartonella with *interspecific space-over overlap* between bobcats and pumas for WS ($\beta = 1.08$, se = 0.77) and FR ($\beta = 5.46$, se = 4.81) bobcats (Table 5); this covariate occurred in the top-ranked models for each model set (Appendix Tables 2 and 10, respectively) with VIVs of 0.33 and 0.70, respectively (Table 4).

Environmental Factors

In contrast to predictions, the environmental covariates evaluating urban and landscape features were not well supported in our models (Tables 4 and 5; Appendix Tables 1 – 15). In general, environmental covariates did not occur in top-ranked models, with the exception of NDVI for FCV in FR pumas, which occurred in the top-ranked model (Appendix Table 15), exhibited a VIV of 0.37 (Tables 4), and was positively related to FCV exposure ($\beta = 3.57$ and se = 3.61; Table 5).

DISCUSSION

We present a framework for evaluating how pathogen exposure in animal populations are influenced by demographic, social interaction (both within and between species), and environmental characteristics. Our conclusions are based on the 4 pathogens that we evaluated and future research will be evaluating exposure to additional pathogens in our system. For wild felid species occurring across a gradient of urbanization, the proportion of individuals exposed to the suite of pathogens that we evaluated was consistent with prior studies (see Methods for a review). Demographic factors helped explain exposure to some pathogens in our study. Specifically, age appeared to be positively related to the exposure to pathogens that are both environmentally transmitted (Toxoplasma) and directly transmitted between animals (FIV), consistent with our predictions and other studies of felid populations (Biek et al. 2006b, Bevins et al. 2012). We also predicted that animals with greater extents of space use would be more likely to interact with other individuals and the landscape (Lewis et al. 2014b), which could lead to a greater probability of pathogen transmission. However, we found weak and equivocal support for the effects of space-use extent. Consistent with predictions, there was some evidence that FIV exposure was correlated with greater space-use extents in FR bobcats, but counter to predictions, FCV exposure was correlated with smaller space-use extents (and *intraspecific space-use overlap*, see below) for WS bobcats.

Social interactions appeared to influence exposure to some pathogens via indirect and direct means of transmission. As predicted, as *intraspecific space-use overlap* increased within bobcat populations, animals were more likely to be exposed to Toxoplasma. Felids may increase marking behavior along territorial boundaries and in areas of sympatry (Sunquist and Sunquist 2002). Because felids are the definitive host of Toxoplasma and excrete oocysts into the

environment via scats (Dubey 2010, Lélu et al. 2010, Gilot-Fromont et al. 2012), areas of shared space use would likely exhibit increased concentrations of Toxoplasma and elevated levels of Toxoplasma in prey. In addition, Toxoplasma likely is present at high concentrations at felid marking locations where animals repeatedly scat and urinate (Gilot-Fromont et al. 2012); because animals revisit these sites and investigate the markings of other animals (both within and between species), animals could experience a relatively high chance of being exposed to Toxoplasma through environmental contamination.

Counter to predictions for directly transmitted pathogens, WS bobcats appeared less likely to be exposed to FCV as *intraspecific space-use overlap* and *space-use extent* (see above) increased, and FR pumas appeared less likely to be exposed to FIV as the number of potential intraspecific interactions (i.e., *degree*) increased. Both *space-use overlap* and *degree* are positively correlated with *space-use extent* (Lewis et al. 2014b), which itself is related to gender and the behavior or resident or transient animals. In wild felids, females and residents generally express smaller extents of space-use than males and transients, which are associated with increased movement extents with less pronounced site fidelity (Sunquist and Sunquist 2002). Although transient animals typically do not have a defined home range and therefore might be less likely to experience strong direct interactions associated with mating and territorial defense behavior (Sunquist and Sunquist 2002), transients could also potentially participate in more frequent aggressive interactions when attempting to establish a resident territory; however, the effect of transient behavior on contact and disease transmission is in need or further study. Within resident individuals, it might be predicted that animals with larger home ranges (e.g., males) would exhibit increased opportunities to interact, resulting in greater exposure to pathogens (Lewis et al. 2014b).

Interspecific space-use overlap appeared to increase exposure to Bartonella in bobcats. It is unknown if bobcats acquired vectors (e.g., fleas or ticks) that transmitted this pathogen from pumas. Increased *interspecific space-use overlap* was possibly related to both felids using similar habitat that might be associated with elevated levels of Bartonella, such as areas associated with domestic cats or other sources (e.g., vectors) of the pathogen (Breitschwerdt and Kordick 2000). Counter to studies in other systems (e.g., Rushton et al. 2000, Franklin et al. 2007), our data did not indicate that the interspecific factors that we evaluated strongly influenced transmission of our four target pathogens between bobcats and pumas.

Environmental variables in our models appeared to have the least support in explaining exposure of the 4 pathogens we evaluated in felid populations. Both the amount of urbanization within extents of space-use for individuals and the forms of urbanization with which animals were associated did not predict exposure to pathogens. Although it is predicted that different forms of urbanization alter prey and domestic cat populations, both of which could be important factors for transmitting pathogens to wild felids (Lélu et al. 2010, Gilot-Fromont et al. 2012), additional research is necessary to quantify how these factors varied across the landscape, especially in relation to feral cat populations and seroprevalence of Toxoplasma in small mammal populations. Further, although directly-transmitted pathogens might be more likely to be transmitted in urbanized landscapes due to increased interactions of felids (Franklin et al. 2007), other research in our study areas reported similar amounts of *interspecific space-use overlap* and potential contact rates in felids across broad scales between urbanized and wildland habitat (Lewis et al. 2014b). In addition, counter to our predictions, NDVI (measuring plant productivity across the landscape; Pettorelli et al. 2005) relative to *space-use extent* did not predict exposure to Toxoplasma and Bartonella. For pathogens that are associated with specific

vectors (e.g., ectoparasites) or intermediate hosts (e.g., small mammals), it could be useful to create predictive maps of habitat association for these organisms (Guerra et al. 2002, Eisen et al. 2003, Eisen et al. 2006a, Eisen et al. 2006b, Vanwambeke et al. 2007b, Eisen and Eisen 2008, Krasnov et al. 2008, Mize et al. 2011) and use this information as covariates in models. Additionally, other environmental factors, such as soil characteristics, can be associated with the risk of disease (Walter et al. 2011b).

There are several factors about our study to consider when interpreting results and conclusions. First, the relatively small number of individuals we were able to screen for pathogens reduced our power to detect difference in exposure to pathogens in relation to covariates (Craft et al. 2009). In addition, misidentification of whether an animal was exposed to a pathogen (i.e., false negatives or false positives) is a common issue in disease ecology and increases uncertainty in results (McClintock et al. 2010) and such implications can be accentuated at relatively small sample sizes. In our study, although we detected low seroprevalence of FIV in bobcats (Bevins et al. 2012), other research utilizing PCR analyses for the same individuals failed to detect the presence of FIV (Lagana et al. 2013); thus, there is ambiguity as to whether bobcats were exposed to FIV in our study. Second, pathogen transmission is often a rare event with myriad factors influencing pathogen exposure. Other factors that could be evaluated to understand exposure of pathogens in felids include habitat characteristics for pathogens and vectors (as explained above), population densities of prey (Lélu et al. 2010, Young et al. 2014) and competitors (Rushton et al. 2000), and composition of the wildlife community (Ostfeld and Holt 2004, Levi et al. 2012). Third, the spatial scale of analysis can strongly influence inference (Forman 1995). Although our study did not find strong results at relatively fine spatial scales, broad-scale analyses of pathogens might better explain patterns

(Craft et al. 2009). At fine scales, patterns might appear as a random process or homogenous, but at broader spatial scales patterns may become more heterogeneous. For example, some vectors, such as ticks, demonstrate a gradient of population densities across their geographic range, where they are most abundant at the interior of their distributional range and decrease in density by 1-2 orders of magnitude at the edge of their range (French 1995); such patterns could affect the opportunity for animals to be exposed to pathogens. In addition, increased parasite loads can occur in species at the edge of their geographic distribution, potentially related to abiotic stresses on animals at the boundaries of their range (Briers 2003).

In addition to providing insight on pathogen exposure in wild felids, importantly, our study provides a conceptual framework for evaluating how demographic, social, and environmental factors influence disease dynamics in animal populations. Such a framework is useful because it allows for the comparison and evaluation of the relative strength among multiple mechanisms and hypotheses. Future work applying this framework to this system and others will be necessary to gain a better understanding about how ecological mechanisms influence pathogen exposure and transmission, with important implications for the conservation of animal populations.

Table 1. Predictions of how demographic, social, and environmental characteristics will influence exposure of pathogens in bobcat and puma populations. The expected relative effect strength of each prediction is included in parentheses.

Pathogen	Demographic	Social	Environment
Toxoplasma gondii	1. Higher prevalence in males and older animals (strong). 2. Higher prevalence as space-use extent increases due to interacting with more of the landscape (moderate).	1. Increased space-use overlap (both intra- and interspecific) increases oocyst presence in environment leading to greater prevalence in prey and increasing opportunity to be infected through environmental contamination (moderate).	1. Animals with more NDVI in their extent of space use will be more likely to be infected (moderate). 2. Greater prevalence in areas of low-density residential development (strong).
Bartonella spp.	1. Higher prevalence in older animals (strong). 2. Higher prevalence as space-use extent increases due to interacting with more of the landscape (moderate).	1. Increased opportunities for intraspecific interactions leads to greater opportunity to transmit fleas (moderate).	1. Animals with more NDVI in their extent of space use will be more likely to be infected (moderate). 2. Greater prevalence in areas of low-density residential and WUI development (strong).
Feline Immunodeficiency Virus (FIV)	1. Higher prevalence in males and older animals (strong). 2. Higher prevalence as space-use extent increases due to interacting with more individuals (moderate).	1. Increased opportunities for intraspecific interactions in both felids (strong) and interspecific interactions for pumas (weak) increases prevalence.	1. Animals will not contract FIV from the environment. However, greater exposure is expected in urbanized areas due to increased interactions.
Feline Calicivirus (FCV)	1. Higher prevalence in males and older animals (strong). 2. Higher prevalence as space-use extent increases due to interacting with more individuals (moderate).	1. Increased opportunities for intra- and interspecific interactions increases prevalence (strong).	1. Unknown. Possibly transmitted indirectly in the environment, particularly in areas of shared space use (weak). 2. Greater exposure is expected in urbanized areas due to increased interactions.

Table 2. Definitions of covariates used in models evaluating pathogens in bobcats and pumas across a gradient of urbanization on the Western Slope (WS) and Front Range (FR) of Colorado. For further explanations of covariates see Methods and Lewis et al. (2014b).

Covariate	**Definition**
Sex	Male or female. For modeling, males = 0 and females = 1.
Age	Continuous measure of age for adult-sized animals estimated based on dental characteristics and body size.
Space-use extent	Spatial extent that animal used based on space-use estimation of utilization distribution using the Brownian bridge movement model or kernel density methods. Because space-use extent is related to sex and age it was grouped with these covariates.
Space-use overlap	Overlap in space use between animals using the utilization distribution overlap index (UDOI) statistic (Fieberg and Kochanny 2005).
Degree	The number of neighbors an individual potentially interacted with based on overlap in space-use extents (Newman 2003, Wey et al. 2008).
In-strength	The sum of space-use overlap values across all neighbors associated with an individual (Godfrey et al. 2010).
Equivalent social connectivity	Equivalent social connectivity (ESC) among animals incorporates space-use overlap and extent (Lewis et al. 2014b). This metric was based on equivalent connectivity (Saura et al. 2011), which was simplified to evaluate for an individual animal as follows: $\mathrm{ESC}_i = \sqrt{\sum_{j=1}^{n} a_i\, a_j p_{ij}^*}$ where a_i is the space-use extent for the focal animal i and a_j are the spatial extent of

	space use for animals j and p_{ij}^{*} is the Bhattacharyya's affinity (BA) statistic (Fieberg and Kochanny 2005) used to define space-use overlap between animals *i* and *j* (Lewis et al. 2014b).
Amount of urbanization in space-use extent	Human occurrence points (HOP; residences and structures) were digitized in ArcMap 10 and a kernel of 1000 m was fit over each HOP and kernels were summed to calculate human influence on the landscape (Lewis et al. 2011). An animal's space-use extent was intersected with this layer and the amount of human influence was summed for each individual.
Grid	Whether an animal was associated with exurban development or wildland grid on the WS or wildland-urban interface or wildland grid on the FR. For modeling, in each study area, urbanized grid = 0 and wildland grid = 1.
Amount of NDVI in space-use extent	The sum of the amount of Normalized difference vegetation index (NDVI; Pettorelli et al. 2005), which measures plant productivity and moisture across the landscape, within an animal's extent of space use. NDVI was evaluated using eMODIS images (USGS August 2009 data on WS and August 2010 data on the FR).
NDVI per area of space-use extent	The amount of NDVI within an animal's space-use extent divided by the area of space use for an individual.

Table 3. Groupings of covariates into five categories (Demographic, Social-Intraspecific, Social-Interspecific, Environment-Urban, Environment-Landscape) used to evaluate pathogens in bobcats and pumas across a gradient of urbanization on the Western Slope (WS) and Front Range (FR) of Colorado. For further explanations of covariates see Methods and Lewis et al. (2014b).

Groupings	Covariates
Demographic	Sex; Age; Space-use extent
Social (Intra- and Interspecific)	Space-use overlap; Degree; In-strength; Equivalent social connectivity
Environment (Urban)	Amoung of urbanization in space-use extent; Grid
Environment (Landscape)	Amount of NDVI in space-use extent; NDVI per area of space-use extent

Table 4. Variable importance values (VIV) for Demographic, Social (intraspecific and interspecific), and Environmental (urban and landscape) categories for bobcats and pumas on the Western Slope (WS) and Front Range (FR) of Colorado, USA. VIV were used to assess the relative importance of groups of covariates in models evaluating pathogens in felid populations. A dash (i.e., -) indicates that models with this covariate could not be evaluated (see Methods).

Study			Demographic			Social Intraspecific		Social Interspecific		Environmental Urban		Environmental Landscape
Area	Species	Pathogen	Sex	Age	Space-Use Extent	Space-Use Overlap	Degree	Space-Use Overlap	Degree	Human Development	Grid	NDVI
WS	Bobcat	Toxoplasma	0.08	0.09	0.09	0.41	0.08	0.09	0.18	0.20	0.08	0.16
WS	Bobcat	Bartonella	0.10	0.13	0.14	0.15	0.13	0.33	0.11	0.20	0.16	0.11
WS	Bobcat	FIV	0.15	0.44	0.14	0.13	0.13	0.14	0.21	0.12	-	0.13
WS	Bobcat	FCV	0.04	0.05	0.42	0.55	0.05	0.16	0.17	0.06	0.08	0.04
WS	Puma	Toxoplasma	-	0.21	-	0.20	-	-	-	-	-	-
WS	Puma	Bartonella	-	-	-	0.13	-	0.12	0.15	0.12	0.12	0.18
WS	Puma	FIV	0.10	0.08	-	0.18	-	0.39	-	0.18	0.08	0.05
WS	Puma	FCV	0.10	-	-	0.26	-	0.13	-	0.19	0.07	0.11
FR	Bobcat	Toxoplasma	0.13	0.34	0.12	0.14	0.13	0.16	0.14	0.13	0.15	0.16
FR	Bobcat	Bartonella	-	0.09	0.03	0.19	0.05	0.70	0.04	0.08	-	0.13
FR	Bobcat	FIV	-	0.06	0.55	0.09	0.21	0.14	0.25	0.13	0.14	0.18
FR	Bobcat	FCV	-	-	-	-	-	-	-	-	-	-
FR	Puma	Toxoplasma	0.15	0.51	-	0.15	0.10	0.13	-	0.12	0.22	0.18
FR	Puma	Bartonella	-	0.15	-	0.30	0.18	0.23	-	0.15	-	0.15
FR	Puma	FIV	0.13	0.09	-	0.07	0.84	0.10	-	0.13	0.06	0.10
FR	Puma	FCV	0.25	0.19	-	0.11	0.13	0.18	-	0.10	0.15	0.37

Table 5. Model-averaged parameter estimates with associated standard errors for Demographic, Social (intraspecific and interspecific), and Environmental (urban and landscape) categories for bobcats and pumas on the Western Slope (WS) and Front Range (FR) of Colorado, USA. A dash (i.e., -) indicates that models with this covariate could not be evaluated (see Methods).

Study			Demographic			Social Intraspecific		Social Interspecific		Environmental Urban		Environmental Landscape
Area	Species	Pathogen	Sex	Age	Space-Use Extent	Space-Use Overlap	Degree	Space-Use Overlap	Degree	Human Development	Grid	NDVI
WS	Bobcat	Toxoplasma	-0.21 (1.02)	-0.11 (0.27)	-0.10 (0.57)	1.06 (0.63)	0.00 (0.52)	0.00 (0.54)	-0.68 (0.68)	0.80 (0.77)	0.46 (1.21)	-0.50 (0.56)
WS	Bobcat	Bartonella	-0.31 (1.07)	0.16 (0.25)	0.42 (0.63)	-0.45 (0.62)	0.57 (0.65)	1.08 (0.77)	-0.31 (0.59)	0.74 (0.57)	-1.10 (1.28)	-0.33 (0.64)
WS	Bobcat	FIV	-1.34 (2.53)	0.71 (0.47)	-0.53 (1.37)	-0.26 (1.15)	-0.31 (0.81)	-0.75 (1.38)	1.50 (1.52)	-0.36 (1.13)	-	0.56 (0.88)
WS	Bobcat	FCV	-0.13 (1.04)	0.08 (0.25)	-1.72 (1.24)	-1.72 (1.26)	0.26 (0.63)	-1.03 (0.95)	-1.53 (1.53)	-0.52 (0.73)	-1.22 (1.35)	0.10 (0.54)
WS	Puma	Toxoplasma	-	1.23 (2.08)	-	1.57 (2.32)	-	-	-	-	-	-
WS	Puma	Bartonella	-	-	-	-0.71 (1.06)	-	0.44 (0.91)	-1.02 (1.59)	-0.43 (1.07)	-0.87 (1.83)	-1.78 (1.96)
WS	Puma	FIV	-0.90 (1.87)	0.19 (0.73)	-	1.50 (1.70)	-	-2.81 (2.42)	-	1.41 (1.11)	0.16 (2.01)	-0.32 (1.21)
WS	Puma	FCV	0.08 (1.66)	-	-	1.52 (1.64)	-	0.27 (0.82)	-	1.14 (1.28)	-1.70 (3.71)	0.03 (1.22)
FR	Bobcat	Toxoplasma	0.55 (1.33)	0.57 (0.44)	-0.03 (0.65)	0.73 (0.88)	-0.22 (0.67)	0.57 (0.75)	-0.49 (0.67)	0.27 (0.68)	1.10 (1.23)	-0.53 (0.74)
FR	Bobcat	Bartonella	-	-1.18 (1.24)	0.76 (1.08)	1.71 (2.61)	1.22 (1.73)	5.46 (4.81)	0.98 (1.11)	-5.02 (4.48)	-	-0.51 (2.29)
FR	Bobcat	FIV	-	-0.05 (0.47)	2.53 (2.34)	0.15 (1.02)	-1.58 (1.55)	-0.83 (0.86)	-3.02 (3.33)	-1.03 (1.97)	-3.52 (4.72)	-2.53 (3.40)
FR	Bobcat	FCV	-	-	-	-	-	-	-	-	-	-
FR	Puma	Toxoplasma	1.08 (1.26)	1.08 (0.69)	-	0.65 (0.76)	-0.14 (0.60)	0.47 (0.63)	-	-0.43 (0.82)	1.65 (1.24)	0.87 (1.02)
FR	Puma	Bartonella	-	0.34 (1.32)	-	2.24 (3.03)	1.30 (2.80)	-2.06 (2.42)	-	-0.39 (1.78)	-	0.66 (1.96)
FR	Puma	FIV	1.44 (1.36)	-0.30 (0.44)	-	0.25 (0.74)	-4.05 (2.79)	0.52 (0.77)	-	0.93 (1.28)	-0.33 (1.28)	0.65 (1.08)
FR	Puma	FCV	1.73 (1.31)	0.47 (0.44)	-	0.23 (0.64)	0.49 (0.76)	0.67 (0.61)	-	0.22 (0.91)	-0.84 (1.17)	3.57 (3.61)

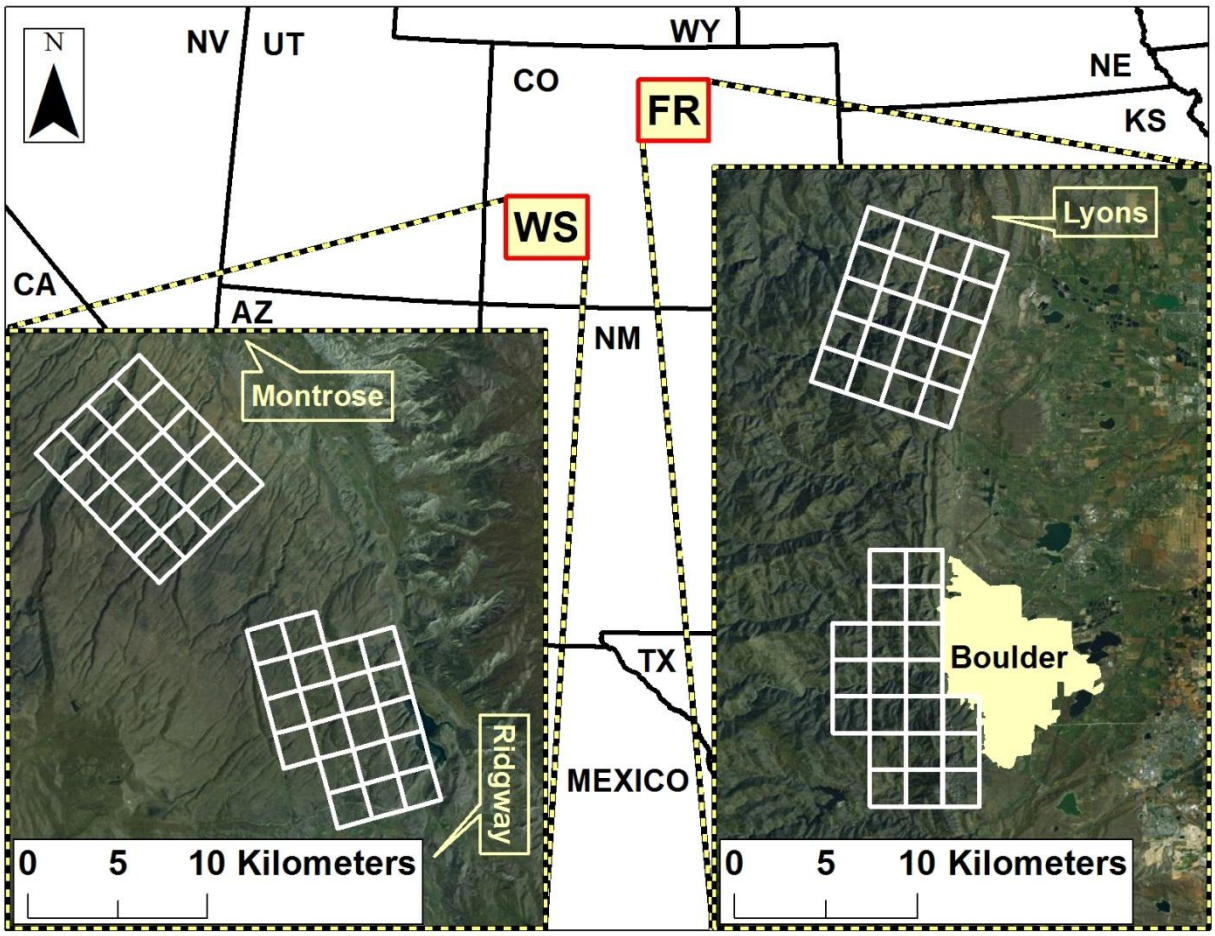
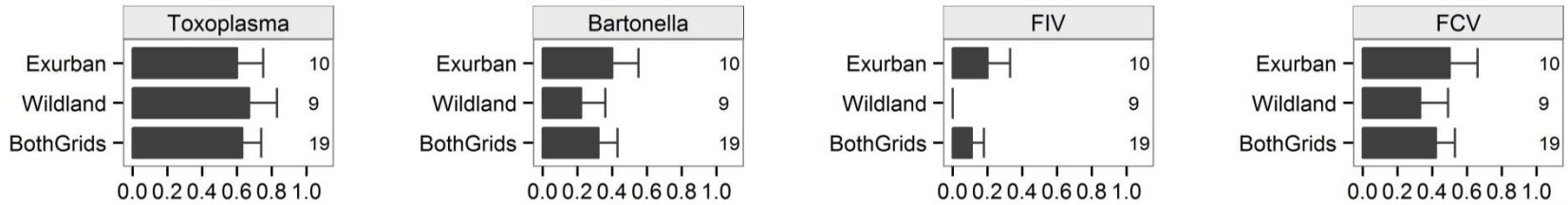
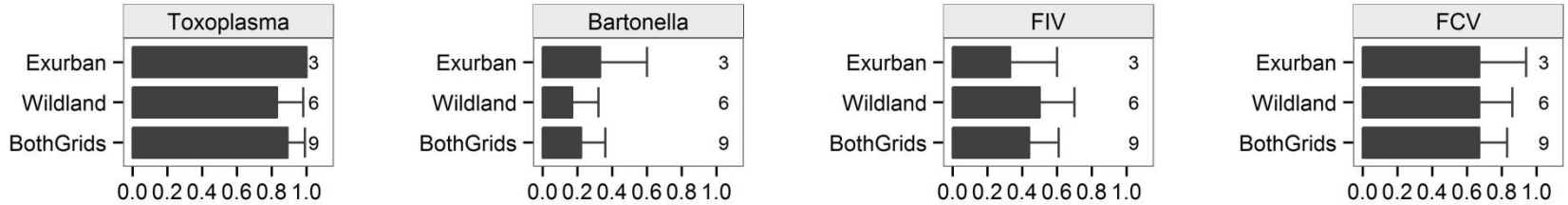


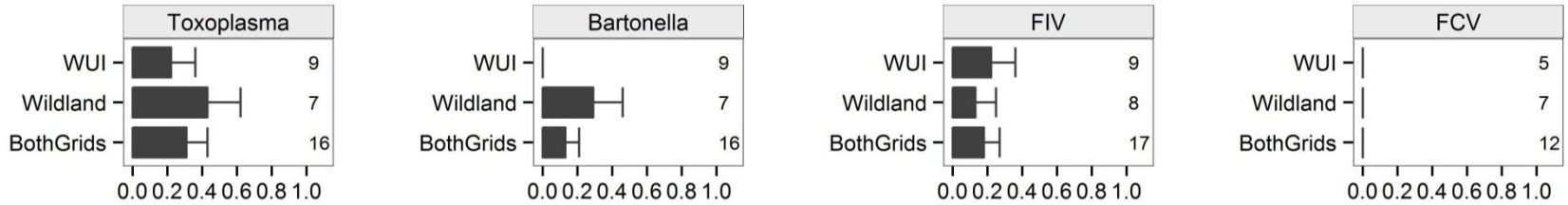
Figure 1. Locations of two study areas in Colorado, USA, which exhibited varying levels of urbanization, where bobcats and pumas were fit with telemetry collars. The more rural Western Slope (WS) was characterized by an exurban development south grid and a wildland north grid during 2009 – 2010. The more urbanized Front Range (FR) study area was characterized by a wildland-urban interface (WUI) south grid and wildland north grid during 2010 – 2012.



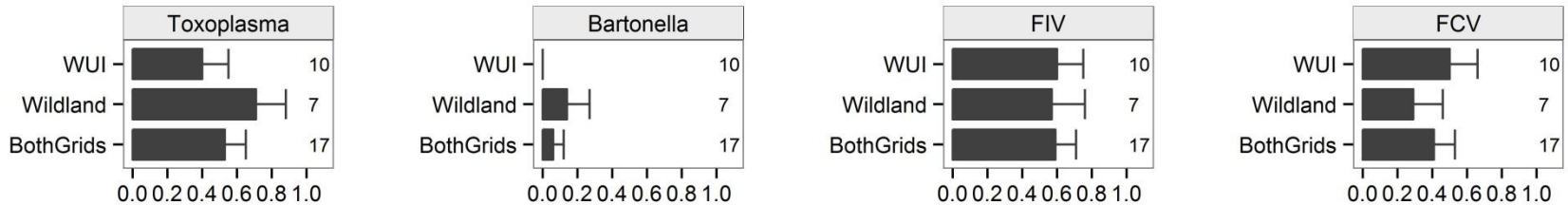
a. WS bobcats



b. WS pumas



c. FR bobcats



d. FR pumas

Figure 2. Prevalence of pathogens (estimates of seroprevalence and 1 standard error) for bobcats (a) and pumas (b) in exurban and wildland habitat on the Western Slope (WS) and for bobcats (c) and pumas (d) in wildland-urban interface (WUI) and wildland habitat on the Front Range (FR), Colorado. Sample sizes for the number of animals screened for antibodies of a pathogen occur on the right side of each figure panel.

LITERATURE CITED

Adler, G. H., and R. Levins. 1994. The island syndrome in rodent populations. Quarterly Review of Biology:473-490.

Afonso, E., E. Germain, M.-L. Poulle, S. Ruette, S. Devillard, L. Say, I. Villena, D. Aubert, and E. Gilot-Fromont. 2013. Environmental determinants of spatial and temporal variations in the transmission of Toxoplasma gondii in its definitive hosts. International Journal for Parasitology: Parasites and Wildlife 2:278-285.

Afonso, E., M. Lemoine, M.-L. Poulle, M.-C. Ravat, S. Romand, P. Thulliez, I. Villena, D. Aubert, M. Rabilloud, and B. Riche. 2008. Spatial distribution of soil contamination by Toxoplasma gondii in relation to cat defecation behaviour in an urban area. International journal for parasitology 38:1017-1023.

Afonso, E., P. Thulliez, and E. Gilot-Fromont. 2010. Local meteorological conditions, dynamics of seroconversion to Toxoplasma gondii in cats (Felis catus) and oocyst burden in a rural environment. Epidemiology and infection 138:1105-1113.

Albrecht, M., and N. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134-141.

Alonso, R. S. 2012. The effects of urbanization and road development on carnivores in southern California. Colorado State University.

Altizer, S., D. Harvell, and E. Friedle. 2003a. Rapid evolutionary dynamics and disease threats to biodiversity. Trends in Ecology & Evolution 18:589-596.

Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. A. Cunnningham, A. P. Dobson, V. Ezenwa, and K. E. Jones. 2003b. Social organization and parasite risk in mammals: integrating theory and empirical studies. Annual Review of Ecology, Evolution, and Systematics 34:517-547.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, NY.

Beckmann, J. P., and J. Berger. 2003. Using black bears to test ideal-free distribution models experimentally. Journal of Mammalogy 84:594-606.

Beier, P., S. P. D. Riley, and R. M. Sauvajot. 2010. Mountain lions (Puma concolor). Pages 141-155 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban carnivores: ecology, conflict and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Bekoff, M. 2001. Observations of scent-marking and discriminating self from others by a domestic dog (Canis familiaris): tales of displaced yellow snow. Behavioural processes 55:75-79.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075-1085.

Bevins, S. N., S. Carver, E. E. Boydston, L. M. Lyren, M. Alldredge, K. A. Logan, S. P. Riley, R. N. Fisher, T. W. Vickers, and W. Boyce. 2012. Three pathogens in sympatric populations of pumas, bobcats, and domestic cats: implications for infectious disease transmission. PLoS One 7:e31403 31401- 31410.

Biek, R., A. J. Drummond, and M. Poss. 2006a. A virus reveals population structure and recent demographic history of its carnivore host. Science 311:538-541.

Biek, R., T. K. Ruth, K. M. Murphy, C. R. Anderson Jr, M. Johnson, R. DeSimone, R. Gray, M. G. Hornocker, C. M. Gillin, and M. Poss. 2006b. Factors associated with pathogen seroprevalence and infection in Rocky Mountain cougars. Journal of wildlife diseases 42:606-615.

Birch, L. C. 1957. The meanings of competition. American Naturalist 91:5-18.

Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soulé. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7:552-563.

Boze, B. G. 2010. Correlates of coprophagy in the domestic dog (Canis familiaris) as assessed by owner reports. Journal of Applied Companion Animal Behavior 4:28-38.

Bradley, C. A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology & Evolution 22:95-102.

Bradley, C. A., S. E. Gibbs, and S. Altizer. 2008. Urban land use predicts West Nile virus exposure in songbirds. Ecological Applications 18:1083-1092.

Brearley, G., J. Rhodes, A. Bradley, G. Baxter, L. Seabrook, D. Lunney, Y. Liu, and C. McAlpine. 2013. Wildlife disease prevalence in human-modified landscapes. Biological Reviews 88:427-442.

Breitschwerdt, E. B., and D. L. Kordick. 2000. Bartonella infection in animals: carriership, reservoir potential, pathogenicity, and zoonotic potential for human infection. Clinical microbiology reviews 13:428-438.

Briers, R. A. 2003. Range limits and parasite prevalence in a freshwater snail. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:S178-S180.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950-2000. Ecological Applications 15:1851-1863.

Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:1-21.

Burgman, M. A., and J. C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation 6:19-28.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition edition. Springer Verlag, New York, NY, USA.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. Ginsberg, M. Griffiths, J. Holden, K. Kawanishi, and M. Kinnaird. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4:75-79.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239-1241.

Caro, T., and C. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67-75.

Carothers, J. H., and F. M. Jaksić. 1984. Time as a niche difference: the role of interference competition. Oikos 42:403-406.

Carver, S., A. V. Scorza, S. N. Bevins, S. P. Riley, K. R. Crooks, S. VandeWoude, and M. R. Lappin. 2012. Zoonotic parasites of bobcats around human landscapes. Journal of clinical microbiology 50:3080-3083.
Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.
Chomel, B. B., R. W. Kasten, J. B. Henn, and S. Molia. 2006. Bartonella infection in domestic cats and wild felids. Annals of the New York Academy of Sciences 1078:410-415.
Chomel, B. B., Y. Kikuchi, J. S. Martenson, M. E. Roelke-Parker, C.-C. Chang, R. W. Kasten, J. E. Foley, J. Laudre, K. Murphy, and P. K. Swift. 2004. Seroprevalence of Bartonella infection in American free-ranging and captive pumas (Felis concolor) and bobcats (Lynx rufus). Veterinary research 35:233-241.
Cohen, J. E. 2003. Human population: the next half century. Science 302:1172-1175.
Cooch, E., and G. White. 2012. Program MARK: a gentle introduction, 11th edition. <http://www.phidot.org/software/mark/docs/book/>.
Craft, M. E., and D. Caillaud. 2011. Network models: an underutilized tool in wildlife epidemiology? Interdisciplinary perspectives on infectious diseases 2011:1-12.
Craft, M. E., E. Volz, C. Packer, and L. A. Meyers. 2009. Distinguishing epidemic waves from disease spillover in a wildlife population. Proceedings of the Royal Society B: Biological Sciences doi:10.1098/rspb. 2008.1636:1-9.
Creel, S., G. Spong, and N. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35-60 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, andR. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge, UK.
Crooks, K., S. Riley, S. Gehrt, T. Gosselink, and T. Van Deelen. 2010. Community ecology of urban carnivores. Pages 185-196 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban carnivores: ecology, conflict, and conservation. The John Hopkins University Press, Baltimore, MD, USA.
Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488-502.
Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation. Cambridge University Press, New York.
Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.
Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. Journal of Mammalogy 56:177-198.
Csardi, G. 2014. igraph. R Core Development Team.
Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience 50:593-601.
Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London.
Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife--threats to biodiversity and human health. Science 287:443-449.
Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2001. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta tropica 78:103-116.
Deplazes, P., F. van Knapen, A. Schweiger, and P. A. Overgaauw. 2011. Role of pet dogs and cats in the transmission of helminthic zoonoses in Europe, with a focus on echinococcosis and toxocarosis. Veterinary parasitology 182:41-53.

Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. The Journal of Wildlife Management 66:1235-1245.
Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. Journal of Ornithology 152:317-323.
Donovan, T. M., M. Freeman, H. Abouelezz, K. Royar, A. Howard, and R. Mickey. 2011. Quantifying home range habitat requirements for bobcats Lynx rufus in Vermont, USA. Biological Conservation 144:2799-2809.
Dubey, J. P. 2010. Toxoplasmosis of animals and humans. CRC Press, Boca Raton, FL.
Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67:370-386.
Dybas, C. L. 2009. Infectious diseases subdue Serengeti lions. BioScience 59:8-13.
Eisen, L., R. Eisen, and R. Lane. 2006a. Geographical distribution patterns and habitat suitability models for presence of host-seeking ixodid ticks in dense woodlands of Mendocino County, California. Journal of medical entomology 43:415-427.
Eisen, R. J., and L. Eisen. 2008. Spatial modeling of human risk of exposure to vector-borne pathogens based on epidemiological versus arthropod vector data. Journal of medical entomology 45:181-192.
Eisen, R. J., L. Eisen, M. B. Castro, and R. S. Lane. 2003. Environmentally related variability in risk of exposure to Lyme disease spirochetes in northern California: effect of climatic conditions and habitat type. Environmental Entomology 32:1010-1018.
Eisen, R. J., R. S. Lane, C. L. Fritz, and L. Eisen. 2006b. Spatial patterns of Lyme disease risk in California based on disease incidence data and modeling of vector-tick exposure. The American journal of tropical medicine and hygiene 75:669-676.
Ellis, M. M., J. S. Ivan, and M. K. Schwartz. 2014. Spatially explicit power analyses for occupancy-based monitoring of wolverine in the US Rocky Mountains. Conservation Biology 28:52-62.
Estrada-Peña, A. 2002. Increasing habitat suitability in the United States for the tick that transmits Lyme disease: a remote sensing approach. Environmental Health Perspectives 110:635-640.
Estrada-Peña, A. n. 2001. Forecasting habitat suitability for ticks and prevention of tick-borne diseases. Veterinary parasitology 98:111-132.
Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399-407.
Farine, D. R., C. J. Garroway, and B. C. Sheldon. 2012. Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. Animal Behaviour 84:1271-1277.
Farnsworth, M. L., L. L. Wolfe, N. T. Hobbs, K. P. Burnham, E. S. Williams, D. M. Theobald, M. M. Conner, and M. W. Miller. 2005. Human land use influences chronic wasting disease prevalence in mule deer. Ecological Applications 15:119-126.
Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325-331.
Fenton, A., J. P. Fairbairn, R. Norman, and P. J. Hudson. 2002. Parasite transmission: reconciling theory and reality. Journal of Animal Ecology 71:893-905.
Ferguson, A. W., N. A. Currit, and F. W. Weckerly. 2009. Isometric scaling in home-range size of male and female bobcats (Lynx rufus). Canadian Journal of Zoology 87:1052-1060.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346-1359.
Flegr, J. 2013. How and why Toxoplasma makes us crazy. Trends in parasitology 29:156-163.
Foley, J. E., P. Swift, K. A. Fleer, S. Torres, Y. A. Girard, and C. K. Johnson. 2013. Risk factors for exposure to felid pathogens in California mountain lions (Puma concolor). Journal of wildlife diseases 49:279-293.
Forman, R. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.
Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. L. France, C. R. Goldman, and K. Heanue. 2002. Road ecology: science and solutions. Island Press, Washington D.C.
Franklin, S., J. Troyer, J. Terwee, L. Lyren, W. Boyce, S. Riley, M. Roelke, K. Crooks, and S. Vandewoude. 2007. Frequent transmission of immunodeficiency viruses among bobcats and pumas. Journal of virology 81:10961-10969.
Franti, C., H. Riemann, D. Behymer, D. Suther, J. Howarth, and R. Ruppanner. 1976. Prevalence of Toxoplasma gondii antibodies in wild and domestic animals in northern California. Journal of the American Veterinary Medical Association 169:901-906.
Freckleton, R., J. Gill, D. Noble, and A. Watkinson. 2005. Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. Journal of Animal Ecology 74:353-364.
French, J. B. 1995. Ixodes scapularis (Acari: Ixodidae) at the edge of its range in southern Wisconsin. Journal of medical entomology 32:876-881.
Fretwell, S. D. 1972. Population in a seasonal environment. Volume 5.Princeton University Press, Princeton, NJ, USA.
Gaston, K. J., T. M. Blackburn, J. J. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37:39-59.
Gause, G. 1934. The struggle for existence. Williams and Wilkins, Baltimore, MD, USA.
Gehrt, S. D., S. P. Riley, and B. L. Cypher. 2010. Urban carnivores: ecology, conflict, and conservation. John Hopkins University Press, Baltimore, MD, USA.
George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107-117.
Germaine, S. S., and B. F. Wakeling. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97:229-237.
Gilot-Fromont, E., M. Lélu, M.-L. Dardé, C. Richomme, D. Aubert, E. Afonso, A. Mercier, C. Gotteland, and I. Villena. 2012. The life cycle of Toxoplasma gondii in the natural environment. Pages 2845 *in* O. D. Djakovic, editor. Toxoplasmosis-Recent Advances InTech. DOI:10.5772/2845.
Gittleman, J. L., S. M. Funk, D. Macdonald, and R. K. Wayne, editors. 2001. Carnivore conservation. Volume 5.Cambridge University Press, Canbridge, UK.
Godfrey, S. S. 2013. Networks and the ecology of parasite transmission: A framework for wildlife parasitology. International Journal for Parasitology: Parasites and Wildlife 2:235-245.
Godfrey, S. S., J. A. Moore, N. J. Nelson, and C. M. Bull. 2010. Social network structure and parasite infection patterns in a territorial reptile, the tuatara (Sphenodon punctatus). International journal for parasitology 40:1575-1585.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia 87:343-348.
Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391:479-481.
Gorman, M. L., and B. J. Trowbridge. 1989. The role of odor in the social lives of carnivores. Pages 57-88 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, New York.
Gotteland, C., Y. Chaval, I. Villena, M. Galan, R. Geers, D. Aubert, M.-L. Poulle, N. Charbonnel, and E. Gilot-Fromont. 2014. Species or local environment, what determines the infection of rodents by Toxoplasma gondii? Parasitology 141:259-268.
Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald, and M. L. Johnson. 2002. Ecological and allometric determinants of home-range size for mountain lions (Puma concolor). Animal Conservation 5:317-324.
Guerra, M., E. Walker, C. Jones, S. Paskewitz, M. R. Cortinas, A. Stancil, L. Beck, M. Bobo, and U. Kitron. 2002. Predicting the risk of Lyme disease: habitat suitability for Ixodes scapularis in the north central United States. Emerging infectious diseases 8:289-297.
Gurnell, J., S. Rushton, P. Lurz, A. Sainsbury, P. Nettleton, M. Shirley, C. Bruemmer, and N. Geddes. 2006. Squirrel poxvirus: landscape scale strategies for managing disease threat. Biological Conservation 131:287-295.
Hadidian, J., S. Prange, R. Rosatte, S. Riley, and S. Gehrt. 2010. Raccoons (Procyon lotor). Pages 35-47 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Hamede, R. K., J. Bashford, H. McCallum, and M. Jones. 2009. Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecology Letters 12:1147-1157.
Hamer, A. J., and K. M. Parris. 2011. Local and landscape determinants of amphibian communities in urban ponds. Ecological Applications 21:378-390.
Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893-1905.
Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.
Harveson, L. A., M. E. Tewes, N. J. Silvy, and J. Rutledge. 2000. Prey use by mountain lions in southern Texas. The Southwestern Naturalist 45:472-476.
Hass, C. C. 2009. Competition and coexistence in sympatric bobcats and pumas. Journal of Zoology 278:174-180.
Hegglin, D., F. Bontadina, P. Contesse, S. Gloor, and P. Deplazes. 2007. Plasticity of predation behaviour as a putative driving force for parasite life-cycle dynamics: the case of urban foxes and Echinococcus multilocularis tapeworm. Functional ecology 21:552-560.
Heilbrun, R. D., N. J. Silvy, M. E. Tewes, and M. J. Peterson. 2003. Using automatically triggered cameras to individually identify bobcats. Wildlife Society Bulletin:748-755.
Hijmans, R. J. 2014. raster. R Core Development Team.
Hines, J. E. 2006. Program PRESENCE. See http://www. mbrpwrc. usgs. gov/software/doc/presence/presence. html.

Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641-648.

_____. 2009. Animal Space Use 1.3 <http://www.cnr.uidaho.edu/population_ecology/animal_space_use>.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges Ecology 88:2354-2363.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. John Wiley & Sons, Hoboken, New Jersey.

Hudson, P., and A. Dobson. 1995. Macroparasites: observed patterns in naturally fluctuating animal populations. Pages 144-176 *in* B. T. Grenfell, andA. P. Dobson, editors. Ecology of infectious diseases in natural populations. Cambridge University Press, Cambridge, UK.

Hugh-Jones, M., N. Barre, G. Nelson, K. Wehnes, J. Warner, J. Garvin, and G. Garris. 1992. Landsat-TM identification of Amblyomma variegatum (Acari: Ixodidae) habitats in Guadeloupe. Remote Sensing of Environment 40:43-55.

Irwin, E. G., and N. E. Bockstael. 2007. The evolution of urban sprawl: evidence of spatial heterogeneity and increasing land fragmentation. Proceedings of the National Academy of Sciences 104:20672-20677.

Karanth, K. U., J. D. Nichols, and N. S. Kumar. 2010. Estimating tiger abundance from camera trap data: field surveys and analytical issues. Pages 97-117 *in* A. F. O'Connell, J. D. Nichols, andK. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Tokyo, Japan.

Keesing, F., L. K. Belden, P. Daszak, A. Dobson, C. D. Harvell, R. D. Holt, P. Hudson, A. Jolles, K. E. Jones, and C. E. Mitchell. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468:647-652.

Kikuchi, Y., B. B. Chomel, R. W. Kasten, J. S. Martenson, P. K. Swift, and S. J. O'Brien. 2004. Seroprevalence of Toxoplasma gondii in American free-ranging or captive pumas (Felis concolor) and bobcats (Lynx rufus). Veterinary parasitology 120:1-9.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:1-42.

Knight, R. L., and K. J. Gutzwiller, editors. 1995. Wildlife and recreationists: coexistence through management and research. Island Press, Washington D.C.

Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy 72:391-396.

Krasnov, B., N. Korallo-Vinarskaya, M. Vinarski, G. Shenbrot, D. Mouillot, and R. Poulin. 2008. Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals. Parasitology 135:229-242.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. Ecology 50:587-607.

Kreeger, T. J., J. M. Arnemo, and J. P. Raath. 2002. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153-181.

Laake, J., and E. Rexstad. 2013. RMark—an alternative approach to building linear models in MARK. *in* E. G. Cooch, andG. C. White, editors. Program MARK:A Gentle Introduction.

Lagana, D. M., J. S. Lee, J. S. Lewis, S. N. Bevins, S. Carver, L. L. Sweanor, R. McBride, C. McBride, K. R. Crooks, and S. VandeWoude. 2013. Characterization of regionally associated Feline Immunodeficiency Virus (FIV) in bobcats (Lynx rufus). Journal of wildlife diseases 49:718-722.

Langlois, J. P., L. Fahrig, G. Merriam, and H. Artsob. 2001. Landscape structure influences continental distribution of hantavirus in deer mice. Landscape Ecology 16:255-266.

Lélu, M., M. Langlais, M.-L. Poulle, and E. Gilot-Fromont. 2010. Transmission dynamics of Toxoplasma gondii along an urban–rural gradient. Theoretical population biology 78:139-147.

Lembeck, M., and G. I. Gould. 1979. Dynamics of harvested and unharvested bobcat populations in California. Pages 53-54 *in* Bobcat Research Conference Proceedings: Current Research on Biology and Management of *Lynx rufus*. National Wildlife Federation Scientific Technical Series 6, Front Royal, VA.

Lenth, B. E., R. L. Knight, and M. E. Brennan. 2008. The effects of dogs on wildlife communities. Natural Areas Journal 28:218-227.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119-1139.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences 109:10942-10947.

Lewis, J. S., L. L. Bailey, S. Vandewoude, and K. R. Crooks. 2014a. Interspecific interactions between wild felids across a gradient of urbanization. PhD Dissertation, Colorado State University.

Lewis, J. S., and K. R. Crooks. 2014. Report to Boulder County Parks and Open Space: Day and night patterns of human recreation and effects on wildlife.

Lewis, J. S., K. A. Logan, M. Alldredge, D. M. Theobald, S. VandeWoude, and K. R. Crooks. 2014b. Contact networks reveal interspecific interactions of sympatric wild felids driven by space use along an urban gradient. PhD Dissertation, Colorado State University.

Lewis, J. S., K. A. Logan, M. W. Alldredge, L. L. Bailey, S. VandeWoude, and K. R. Crooks. 2014c. Population density and occupancy of wild felids across a gradient of urbanization. PhD Dissertation, Colorado State University.

Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. Landscape and Urban Planning 101:99-107.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413-418.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C.

Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105-117 *in* M. Hornocker, andS. Negri, editors. Cougar ecology and conservation University of Chicago Press, Chicago, Illinois.

Lukacs, P. M., K. P. Burnham, and D. R. Anderson. 2010. Model selection bias and Freedman's paradox. Annals of the Institute of Statistical Mathematics 62:117-125.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.
_____. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton, NJ.
MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461-467.
MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, R. Andrew, J, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.
MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, CA.
MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114.
Magle, S. B., V. M. Hunt, M. Vernon, and K. R. Crooks. 2012. Urban wildlife research: past, present, and future. Biological Conservation 155:23-32.
Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Boston, MA.
McCallum, H. 2008. Landscape structure, disturbance, and disease dynamics. Pages 100-122 *in* R. S. Ostfeld, F. Keesing, andV. T. Eviner, editors. Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems. Princeton University Press, Princeton, NJ.
McClintock, B. T. 2012. Mark-resight models. Pages 18-11 to 18-37 *in* E. Cooch, andG. White, editors. Program MARK: a gentle introduction, 11th edition. <http://www.phidot.org/software/mark/docs/book/>.
McClintock, B. T., J. D. Nichols, L. L. Bailey, D. I. MacKenzie, W. Kendall, and A. B. Franklin. 2010. Seeking a second opinion: uncertainty in disease ecology. Ecology Letters 13:659-674.
McClintock, B. T., and G. C. White. 2012. From NOREMARK to MARK: software for estimating demographic parameters using mark–resight methodology. Journal of Ornithology 152:641-650.
McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009. Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237-246.
McDonald, R. I., P. Kareiva, and R. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695-1703.
McDonnell, M. J., and A. K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23:1143-1155.
McDonnell, M. J., and S. T. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232-1237.
McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883-890.
McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247-260.

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban ecosystems 11:161-176.
McMichael, A. J. 2004. Environmental and social influences on emerging infectious diseases: past, present and future. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 359:1049-1058.
Meredith, M., and M. Ridout. 2013. Overlap. R Core Development Team.
Merenlender, A. M., S. E. Reed, and K. L. Heise. 2009. Exurban development influences woodland bird composition. Landscape and Urban Planning 92:255-263.
Merkle, J., D. Stahler, and D. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56-63.
Milinski, M. 1988. Games fish play: making decisions as a social forager. Trends in Ecology & Evolution 3:325-330.
Mize, E. L., J. I. Tsao, and B. A. Maurer. 2011. Habitat correlates with the spatial distribution of ectoparasites on Peromyscus leucopus in southern Michigan. Journal of Vector Ecology 36:308-320.
Monello, R. J., and M. E. Gompper. 2009. Relative importance of demographics, locale, and seasonality underlying louse and flea parasitism of raccoons (Procyon lotor). Journal of Parasitology 95:56-62.
Morse, D. H. 1974. Niche breadth as a function of social dominance. American Naturalist 108:818-830.
Morse, S. S. 1995. Factors in the emergence of infectious diseases. Emerging infectious diseases 1:7-15.
Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution 10:58-62.
Murray, D. L., C. A. Kapke, J. F. Evermann, and T. K. Fuller. 1999. Infectious disease and the conservation of free-ranging large carnivores. Animal Conservation 2:241-254.
Naugle, D. E., and M. S. Boyce. 2011. Energy development and wildlife conservation in western North America. Island Press, Washington D.C.
Nelson, A. C., and T. W. Sanchez. 2005. The effectiveness of urban containment regimes in reducing exurban sprawl. The Planning Review 41:42-47.
Newman, M. E. 2003. The structure and function of complex networks. SIAM review 45:167-256.
Nickerson, C., R. Ebel, A. Borchers, and F. Carriazo. 2011. Major uses of land in the United States, 2007. United States Department of Agriculture, Economic Research Service.
Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology 26:432-441.
Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949-963.
O'Connell, A. F., J. D. Nichols, and U. K. Karanth. 2010. Camera traps in animal ecology: Methods and analyses. Springer Verlag, Tokyo, Japan.
Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and the Environment 2:13-20.
Ottaviani, D., S. C. Cairns, M. Oliverio, and L. Boitani. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. Journal of Zoology 269:317-330.

Page, L. K., S. D. Gehrt, and N. P. Robinson. 2008. Land-use effects on prevalence of raccoon roundworm (Baylisascaris procyonis). Journal of wildlife diseases 44:594-599.
Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492-508.
Paul-Murphy, J., T. Work, D. Hunter, E. McFie, and D. Fjelline. 1994. Serologic survey and serum biochemical reference ranges of the free-ranging mountain lion (Felis concolor) in California. Journal of wildlife diseases 30:205-215.
Paull, S. H., S. Song, K. M. McClure, L. C. Sackett, A. M. Kilpatrick, and P. T. Johnson. 2012. From superspreaders to disease hotspots: linking transmission across hosts and space. Frontiers in Ecology and the Environment 10:75-82.
Pecon-Slattery, J., J. L. Troyer, W. E. Johnson, and S. J. O'Brien. 2008. Evolution of feline immunodeficiency virus in Felidae: implications for human health and wildlife ecology. Veterinary immunology and immunopathology 123:32-44.
Pedersen, A. B., K. E. Jones, C. L. Nunn, and S. Altizer. 2007. Infectious diseases and extinction risk in wild mammals. Conservation Biology 21:1269-1279.
Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? The American Naturalist 126:261-266.
Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503-510.
Plowright, R. K., S. H. Sokolow, M. E. Gorman, P. Daszak, and J. E. Foley. 2008. Causal inference in disease ecology: investigating ecological drivers of disease emergence. Frontiers in Ecology and the Environment 6:420-429.
Polfus, J. L., and P. R. Krausman. 2012. Impacts of residential development on ungulates in the Rocky Mountain West. Wildlife Society Bulletin 36:647-657.
Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual review of ecology and systematics 20:297-330.
Pollock, J. F. 2006. Detecting population peclines over large areas with presence-absence, time-to-encounter, and count survey methods. Conservation Biology 20:882-892.
Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. The Journal of Wildlife Management 67:324-333.
Quigley, H., and M. Hornocker. 2009. Cougar population dynamics. Pages 59-75 *in* M. Hornocker, andS. Negri, editors. Cougar: ecology and conservation. University of Chicago Press, Chicago, Ilinois.
R. Development Core Team 2014. R: a language and environment for statistical computing, Version 3.0.2. R Foundation for Statistical Computing. Vienna, Austria.
Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. Ecological Applications 15:799-805.
Radford, A. D., K. P. Coyne, S. Dawson, C. J. Porter, and R. M. Gaskell. 2007. Feline calicivirus. Veterinary research 38:319-335.
Ralls, K. 1971. Mammalian scent marking. Science 171:443-449.
Ramsey, D., N. Spencer, P. Caley, M. Efford, K. Hansen, M. Lam, and D. Cooper. 2002. The effects of reducing population density on contact rates between brushtail possums:

implications for transmission of bovine tuberculosis. Journal of Applied Ecology 39:806-818.
Reperant, L., D. Hegglin, I. Tanner, C. Fischer, and P. Deplazes. 2009. Rodents as shared indicators for zoonotic parasites of carnivores in urban environments. Parasitology 136:329-337.
Reperant, L. A., D. Hegglin, C. Fischer, L. Kohler, J.-M. Weber, and P. Deplazes. 2007. Influence of urbanization on the epidemiology of intestinal helminths of the red fox (Vulpes vulpes) in Geneva, Switzerland. Parasitology research 101:605-611.
Richmond, O. M., J. E. Hines, and S. R. Beissinger. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecological Applications 20:2036-2046.
Ridout, M., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322-337.
Riem, J. G., R. B. Blair, D. N. Pennington, and N. G. Solomon. 2012. Estimating mammalian species diversity across an urban gradient. The American midland naturalist 168:315-332.
Riley, S., E. Boydston, K. Crooks, and L. Lyren. 2010. Bobcats (Lynx rufus). Pages 121-138 *in* S. D. Gehrt, S. P. D. Riley, andB. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, MD.
Riley, S. P. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. Journal of Wildlife Management 70:1425-1435.
Riley, S. P., J. Foley, and B. Chomel. 2004. Exposure to feline and canine pathogens in bobcats and gray foxes in urban and rural zones of a national park in California. Journal of wildlife diseases 40:11-22.
Riley, S. P., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566-576.
Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733-1741.
Robert, K., D. Garant, and F. Pelletier. 2012. Keep in touch: does spatial overlap correlate with contact rate frequency? The Journal of Wildlife Management 76:1670-1675.
Roelke, M. E., D. J. Forrester, E. R. Jacobson, G. V. Kollias, F. W. Scott, M. C. Barr, J. F. Evermann, and E. C. Pirtle. 1993. Seroprevalence of infectious disease agents in free-ranging Florida panthers (Felis concolor coryi). Journal of wildlife diseases 29:36-49.
Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47:602-612.
_____. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, United Kingdom.
Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011-1017.
Royle, A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.
Royle, J. A., J. D. Nichols, and M. Kéry. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110:353-359.

Ruell, E. W., S. P. Riley, M. R. Douglas, J. P. Pollinger, and K. R. Crooks. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture-recapture sampling. Journal of Mammalogy 90:129-135.

Rushton, S., P. Lurz, J. Gurnell, and R. Fuller. 2000. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? Journal of Applied Ecology 37:997-1012.

Russell, C. A., D. L. Smith, L. A. Waller, J. E. Childs, and L. A. Real. 2004. A priori prediction of disease invasion dynamics in a novel environment. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:21-25.

Ruth, T. K., and K. Murphy. 2010. Cougar-prey relationships. Pages 138-162 *in* M. Hornocker, andS. Negri, editors. Cougar: ecology and conservation. University of Chicago Press, Chicago, IL.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, and A. Kinzig. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY.

Saura, S., C. Estreguil, C. Mouton, and M. Rodríguez-Freire. 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). Ecological Indicators 11:407-416.

Saura, S., and L. Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning 83:91-103.

Schauber, E. M., D. J. Storm, and C. K. Nielsen. 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. The Journal of Wildlife Management 71:155-163.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103-113.

Schneider, A., M. Friedl, and D. Potere. 2009. A new map of global urban extent from MODIS satellite data. Environmental Research Letters 4:1-11.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

_____. 1982. The controversy over interspecific competition. American Scientist 70:586-595.

_____. 1983. Field experiments on interspecific competition. American Naturalist 122:240-285.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:1-60.

Seimon, T., D. Miquelle, T. Chang, A. Newton, I. Korotkova, G. Ivanchuk, E. Lyubchenko, A. Tupikov, E. Slabe, and D. McAloose. 2013. Canine distemper virus: an emerging disease in wild endangered Amur tigers. mBio:doi:10.1128/mBio.00410-00413.

Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. A meta-analysis of global urban land expansion. PLoS One 6:1-9.

Seto, K. C., B. Güneralp, and L. R. Hutyra. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences 109:16083-16088.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186-191.
Siikamäki, P., and K. Kangas. 2009. Limits of acceptable change as a tool for protected area management—Oulanka National Park as an example. Research and monitoring of sustainability of nature-based tourism and recreational use of nature in Oulanka and Paanajärvi National Parks, Oulanka Reports 29:35-52.
Skelly, D. K., S. R. Bolden, M. P. Holland, L. Freidenburg, N. Freidenfelds, T. R. Malcolm, S. Collinge, and C. Ray. 2006. Urbanization and disease in amphibians. Pages 153-167 *in* Disease ecology: community structure and pathogen dynamics.
Smith, D. L., B. Lucey, L. A. Waller, J. E. Childs, and L. A. Real. 2002. Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. Proceedings of the National Academy of Sciences 99:3668-3672.
Soave, O., and C. Brand. 1991. Coprophagy in animals: a review. The Cornell Veterinarian 81:357-364.
Soulsbury, C., P. Baker, G. Iossa, and S. Harris. 2010. Red foxes (Vulpes vulpes). Pages 63-78 *in* S. Gehrt, S. Riley, andB. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. Johns Hopkins University Press, Baltimore, Maryland.
Strayer, D. L. 1999. Statistical power of presence-absence data to detect population declines. Conservation Biology 13:1034-1038.
Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, IL, USA.
Temple, D., and R. Gutiérrez. 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conservation Biology 27:1087-1095.
Terborgh, J., and J. A. Estes. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington D.C.
Theobald, D. M. 2004. Placing exurban land-use change in a human modification framework. Frontiers in Ecology and the Environment 2:139-144.
Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society 10:1-34.
Theobald, D. M., and W. H. Romme. 2007. Expansion of the US wildland-urban interface. Landscape and Urban Planning 83:340-354.
Tompkins, D. M., A. M. Dunn, M. J. Smith, and S. Telfer. 2011. Wildlife diseases: from individuals to ecosystems. Journal of Animal Ecology 80:19-38.
Totton, S. C., R. R. Tinline, R. C. Rosatte, and L. L. Bigler. 2002. Contact rates of raccoons (Procyon lotor) at a communal feeding site in rural eastern Ontario. Journal of wildlife diseases 38:313-319.
Tracey, J. A. 2014. mkde. R Core Development Team.
Tracey, J. A., S. N. Bevins, S. VandeWoude, and K. R. Crooks. 2014. An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. Ecosphere 5:1-24.
Tracey, J. A., J. Zhu, E. Boydston, L. Lyren, R. N. Fisher, and K. R. Crooks. 2013. Mapping behavioral landscapes for animal movement: a finite mixture modeling approach. Ecological Applications 23:654-669.
Troyer, J. L., J. Pecon-Slattery, M. E. Roelke, W. Johnson, S. VandeWoude, N. Vazquez-Salat, M. Brown, L. Frank, R. Woodroffe, and C. Winterbach. 2005. Seroprevalence and

genomic divergence of circulating strains of feline immunodeficiency virus among Felidae and Hyaenidae species. Journal of virology 79:8282-8294.
Troyer, J. L., S. VandeWoude, J. Pecon-Slattery, C. McIntosh, S. Franklin, A. Antunes, W. Johnson, and S. J. O'Brien. 2008. FIV cross-species transmission: an evolutionary prospective. Veterinary immunology and immunopathology 123:159-166.
Vander Wal, E., M. P. Laforge, and P. D. McLoughlin. 2014. Density dependence in social behaviour: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. Behavioral Ecology and Sociobiology 68:383-390.
VanderWaal, K. L., H. Wang, B. McCowan, H. Fushing, and L. A. Isbell. 2014. Multilevel social organization and space use in reticulated giraffe (Giraffa camelopardalis). Behavioral Ecology 25:17-26.
VandeWoude, S., and C. Apetrei. 2006. Going wild: lessons from naturally occurring T-lymphotropic lentiviruses. Clinical microbiology reviews 19:728-762.
Vanwambeke, S. O., E. F. Lambin, M. P. Eichhorn, S. P. Flasse, R. E. Harbach, L. Oskam, P. Somboon, S. van Beers, B. H. van Benthem, and C. Walton. 2007a. Impact of land-use change on dengue and malaria in northern Thailand. EcoHealth 4:37-51.
Vanwambeke, S. O., P. Somboon, R. E. Harbach, M. Isenstadt, E. F. Lambin, C. Walton, and R. K. Butlin. 2007b. Landscape and land cover factors influence the presence of Aedes and Anopheles larvae. Journal of medical entomology 44:133-144.
Vaske, J. J., L. B. Shelby, and M. P. Donnelly. 2009. Estimating visitation to Boulder Open Space and Mountain Parks. (HDNRU Report No. 80) Report for Boulder Open Space and Mountain Parks: Colorado State University, Human Dimensions of Natural Resources.
Walter, W. D., J. W. Fischer, S. Baruch-Mordo, and K. C. VerCauteren. 2011a. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. Pages 249-268 *in* K. Ondrej, editor. Modern telemetry. http://www.intechopen.com/books/show/title/modern-telemetry, InTech Open Access.
Walter, W. D., D. P. Walsh, M. L. Farnsworth, D. L. Winkelman, and M. W. Miller. 2011b. Soil clay content underlies prion infection odds. Nature communications 2:200.
Wey, T., D. T. Blumstein, W. Shen, and F. Jordán. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal Behaviour 75:333-344.
Wheeler, D. C., L. A. Waller, and R. Biek. 2010. Spatial analysis of feline immunodeficiency virus infection in cougars. Spatial and spatio-temporal epidemiology 1:151-161.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46:120-139.
White, G. C., and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329-350 *in* J. Millspaugh, andJ. Marzluff, editors. Design and analysis of wildlife radiotelemetry studies. Academic Press, San Diego, California, USA.
Wiens, J. A. 1977. On competition and variable environment. American Scientist 65:590-597.
Wilcox, B. A., and D. J. Gubler. 2005. Disease ecology and the global emergence of zoonotic pathogens. Environmental Health and Preventive Medicine 10:263-272.
Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.
Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS One 8:e60590.

Wilson, K., O. Bjørnstad, A. Dobson, S. Merler, G. Poglayen, S. Randolph, A. Read, and A. Skorping. 2002. Heterogeneities in macroparasite infections: patterns and processes. Pages 6-44 *in* P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, andA. P. Dobson, editors. The ecology of wildlife diseases. Oxford University Press, Oxford.

Woolhouse, M. E., C. Dye, J.-F. Etard, T. Smith, J. Charlwood, G. Garnett, P. Hagan, J. Hii, P. Ndhlovu, and R. Quinnell. 1997. Heterogeneities in the transmission of infectious agents: implications for the design of control programs. Proceedings of the National Academy of Sciences 94:338-342.

Woolhouse, M. E., D. T. Haydon, and R. Antia. 2005. Emerging pathogens: the epidemiology and evolution of species jumps. Trends in Ecology & Evolution 20:238-244.

Wyatt, T. D. 2014. Pheromones and animal behaviour: chemical signals and signatures (second edition). Cambridge University Press, Cambridge, United Kingdom.

Yamamoto, K., B. B. Chomel, L. J. Lowenstine, Y. Kikuchi, L. G. Phillips, B. C. Barr, P. K. Swift, K. R. Jones, S. P. Riley, and R. W. Kasten. 1998. Bartonella henselae antibody prevalence in free-ranging and captive wild felids from California. Journal of wildlife diseases 34:56-63.

Young, H. S., R. Dirzo, K. M. Helgen, D. J. McCauley, S. A. Billeter, M. Y. Kosoy, L. M. Osikowicz, D. J. Salkeld, T. P. Young, and K. Dittmar. 2014. Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. Proceedings of the National Academy of Sciences 111:7036-7041.

Zuk, M., and K. A. McKean. 1996. Sex differences in parasite infections: patterns and processes. International journal for parasitology 26:1009-1024.

Appendix Table 1. Toxoplasma in bobcats on the Western Slope of Colorado, USA.

#	Model	K	AICc	Δ AICc	ω	LL
5	S Intra space use overlap	2	25.94	0.00	0.12	-10.59
1	Intercept	1	27.24	1.31	0.06	-12.50
8	S Inter degree	2	27.97	2.03	0.04	-11.61
39	S Intra space use overlap + E Urban human development	3	27.99	2.05	0.04	-10.19
22	D age + S Intra space use overlap	3	28.22	2.29	0.04	-10.31
9	E Urban human development	2	28.42	2.48	0.03	-11.83
41	S Intra space use overlap + E Landscape NDVI	3	28.45	2.51	0.03	-10.43
11	E Landscape NDVI	2	28.65	2.72	0.03	-11.95
51	S Inter degree + E Urban human development	3	28.67	2.73	0.03	-10.53
40	S Intra space use overlap + E Urban grid	3	28.67	2.74	0.03	-10.54
37	S Intra space use overlap + S Inter space use overlap	3	28.70	2.77	0.03	-10.55
38	S Intra space use overlap + S Inter degree	3	28.70	2.77	0.03	-10.55
29	D space use extent + S Intra space use overlap	3	28.75	2.81	0.03	-10.58
14	D sex + S Intra space use overlap	3	28.78	2.85	0.03	-10.59
36	S Intra space use overlap + S Intra degree	3	28.79	2.85	0.03	-10.59
55	E Urban human development + E Landscape NDVI	3	29.55	3.61	0.02	-10.97
4	D space use extent	2	29.63	3.69	0.02	-12.44
10	E Urban grid	2	29.67	3.73	0.02	-12.46
2	D sex	2	29.67	3.73	0.02	-12.46
3	D age	2	29.68	3.75	0.02	-12.47
7	S Inter space use overlap	2	29.73	3.79	0.02	-12.49
54	E Urban human development + E Urban grid	3	29.74	3.80	0.02	-11.07
6	S Intra degree	2	29.76	3.82	0.02	-12.50
53	S Inter degree + E Landscape NDVI	3	30.55	4.61	0.02	-11.48
32	D space use extent + S Inter degree	3	30.58	4.64	0.01	-11.49
33	D space use extent + E Urban human development	3	30.60	4.67	0.01	-11.50
43	S Intra degree + S Inter degree	3	30.69	4.75	0.01	-11.54
47	S Inter space use overlap + S Inter degree	3	30.78	4.84	0.01	-11.59
25	D age + S Inter degree	3	30.79	4.85	0.01	-11.59
52	S Inter degree + E Urban grid	3	30.79	4.86	0.01	-11.60
17	D sex + S Inter degree	3	30.80	4.86	0.01	-11.60
26	D age + E Urban human development	3	31.09	5.15	0.01	-11.75
35	D space use extent + E Landscape NDVI	3	31.16	5.22	0.01	-11.78
44	S Intra degree + E Urban human development	3	31.19	5.25	0.01	-11.79
18	D sex + E Urban human development	3	31.20	5.26	0.01	-11.80
48	S Inter space use overlap + E Urban human development	3	31.23	5.29	0.01	-11.82
20	D sex + E Landscape NDVI	3	31.31	5.37	0.01	-11.85
56	E Urban grid + E Landscape NDVI	3	31.38	5.45	0.01	-11.89
50	S Inter space use overlap + E Landscape NDVI	3	31.49	5.55	0.01	-11.94
46	S Intra degree + E Landscape NDVI	3	31.50	5.56	0.01	-11.95
28	D age + E Landscape NDVI	3	31.50	5.56	0.01	-11.95
31	D space use extent + S Inter space use overlap	3	32.22	6.28	0.01	-12.31

Appendix Table 2. Bartonella in bobcats on the Western Slope of Colorado, USA.

#	Model	K	AICc	ΔAICc	ω	LL
7	S Inter space use overlap	2	25.15	0.00	0.09	-10.20
1	Intercept	1	25.93	0.79	0.06	-11.85
9	E Urban human development	2	26.18	1.03	0.05	-10.71
49	S Inter space use overlap + E Urban grid	3	26.66	1.51	0.04	-9.53
37	S Intra space use overlap + S Inter space use overlap	3	26.96	1.81	0.04	-9.68
48	S Inter space use overlap + E Urban human development	3	27.07	1.92	0.03	-9.73
6	S Intra degree	2	27.13	1.98	0.03	-11.19
4	D space use extent	2	27.45	2.30	0.03	-11.35
24	D age + S Inter space use overlap	3	27.50	2.36	0.03	-9.95
10	E Urban grid	2	27.74	2.60	0.02	-11.50
16	D sex + S Inter space use overlap	3	27.76	2.61	0.02	-10.08
47	S Inter space use overlap + S Inter degree	3	27.83	2.68	0.02	-10.12
42	S Intra degree + S Inter space use overlap	3	27.93	2.79	0.02	-10.17
31	D space use extent + S Inter space use overlap	3	27.97	2.83	0.02	-10.19
50	S Inter space use overlap + E Landscape NDVI	3	27.99	2.84	0.02	-10.19
3	D age	2	28.11	2.96	0.02	-11.68
5	S Intra space use overlap	2	28.13	2.99	0.02	-11.69
39	S Intra space use overlap + E Urban human development	3	28.16	3.01	0.02	-10.28
11	E Landscape NDVI	2	28.19	3.05	0.02	-11.72
8	S Inter degree	2	28.33	3.18	0.02	-11.79
44	S Intra degree + E Urban human development	3	28.37	3.23	0.02	-10.39
2	D sex	2	28.42	3.28	0.02	-11.84
45	S Intra degree + E Urban grid	3	28.48	3.34	0.02	-10.44
55	E Urban human development + E Landscape NDVI	3	28.51	3.37	0.02	-10.46
33	D space use extent + E Urban human development	3	28.65	3.50	0.02	-10.52
26	D age + E Urban human development	3	28.79	3.65	0.01	-10.60
51	S Inter degree + E Urban human development	3	28.87	3.72	0.01	-10.63
56	E Urban grid + E Landscape NDVI	3	28.94	3.80	0.01	-10.67
32	D space use extent + S Inter degree	3	29.00	3.86	0.01	-10.70
18	D sex + E Urban human development	3	29.02	3.87	0.01	-10.71
54	E Urban human development + E Urban grid	3	29.02	3.88	0.01	-10.71
34	D space use extent + E Urban grid	3	29.21	4.07	0.01	-10.81
43	S Intra degree + S Inter degree	3	29.42	4.28	0.01	-10.91
23	D age + S Intra degree	3	29.48	4.33	0.01	-10.94
30	D space use extent + S Intra degree	3	29.67	4.52	0.01	-11.03
36	S Intra space use overlap + S Intra degree	3	29.77	4.63	0.01	-11.09
46	S Intra degree + E Landscape NDVI	3	29.79	4.65	0.01	-11.10
21	D age + D space use extent	3	29.81	4.67	0.01	-11.11
15	D sex + S Intra degree	3	29.93	4.78	0.01	-11.16
13	D sex + D space use extent	3	29.97	4.82	0.01	-11.19
35	D space use extent + E Landscape NDVI	3	30.20	5.05	0.01	-11.30
29	D space use extent + S Intra space use overlap	3	30.21	5.07	0.01	-11.31
38	S Intra space use overlap + S Inter degree	3	30.25	5.11	0.01	-11.33
40	S Intra space use overlap + E Urban grid	3	30.26	5.12	0.01	-11.33
28	D age + E Landscape NDVI	3	30.38	5.24	0.01	-11.39
52	S Inter degree + E Urban grid	3	30.38	5.24	0.01	-11.39
22	D age + S Intra space use overlap	3	30.48	5.34	0.01	-11.44
41	S Intra space use overlap + E Landscape NDVI	3	30.49	5.34	0.01	-11.45
27	D age + E Urban grid	3	30.53	5.39	0.01	-11.47
19	D sex + E Urban grid	3	30.58	5.44	0.01	-11.49
25	D age + S Inter degree	3	30.77	5.63	0.01	-11.59
12	D sex + D age	3	30.81	5.66	0.01	-11.61
14	D sex + S Intra space use overlap	3	30.93	5.78	0.01	-11.66

Appendix Table 3. FIV in bobcats on the WS

#	Model	K	AICc	ΔAICc	ω	LL
3	D age	2	14.10	0.00	0.12	-4.68
1	Intercept	1	15.02	0.92	0.08	-6.39
25	D age + S Inter degree	3	15.47	1.37	0.06	-3.94
12	D sex + D age	3	15.59	1.48	0.06	-3.99
8	S Inter degree	2	16.09	1.99	0.05	-5.67
22	D age + S Intra space use overlap	3	16.29	2.19	0.04	-4.35
24	D age + S Inter space use overlap	3	16.57	2.47	0.04	-4.49
26	D age + E Urban human development	3	16.66	2.56	0.03	-4.53
11	E Landscape NDVI	2	16.77	2.67	0.03	-6.01
28	D age + E Landscape NDVI	3	16.86	2.75	0.03	-4.63
23	D age + S Intra degree	3	16.89	2.79	0.03	-4.65
21	D age + D space use extent	3	16.91	2.80	0.03	-4.65
32	D space use extent + S Inter degree	3	17.04	2.94	0.03	-4.72
7	S Inter space use overlap	2	17.09	2.98	0.03	-6.17
6	S Intra degree	2	17.37	3.26	0.02	-6.31
4	D space use extent	2	17.47	3.37	0.02	-6.36
9	E Urban human development	2	17.49	3.39	0.02	-6.37
2	D sex	2	17.53	3.43	0.02	-6.39
5	S Intra space use overlap	2	17.53	3.43	0.02	-6.39
43	S Intra degree + S Inter degree	3	18.26	4.16	0.02	-5.33
38	S Intra space use overlap + S Inter degree	3	18.43	4.33	0.01	-5.42
47	S Inter space use overlap + S Inter degree	3	18.50	4.40	0.01	-5.45
53	S Inter degree + E Landscape NDVI	3	18.62	4.51	0.01	-5.51
51	S Inter degree + E Urban human development	3	18.62	4.52	0.01	-5.51
17	D sex + S Inter degree	3	18.83	4.73	0.01	-5.61
50	S Inter space use overlap + E Landscape NDVI	3	19.46	5.36	0.01	-5.93
46	S Intra degree + E Landscape NDVI	3	19.48	5.37	0.01	-5.94
55	E Urban human development + E Landscape NDVI	3	19.50	5.40	0.01	-5.95
41	S Intra space use overlap + E Landscape NDVI	3	19.57	5.46	0.01	-5.98
35	D space use extent + E Landscape NDVI	3	19.60	5.50	0.01	-6.00
20	D sex + E Landscape NDVI	3	19.62	5.52	0.01	-6.01
37	S Intra space use overlap + S Inter space use overlap	3	19.91	5.81	0.01	-6.15
31	D space use extent + S Inter space use overlap	3	19.92	5.82	0.01	-6.16
48	S Inter space use overlap + E Urban human development	3	19.92	5.82	0.01	-6.16
42	S Intra degree + S Inter space use overlap	3	19.94	5.83	0.01	-6.17
16	D sex + S Inter space use overlap	3	19.94	5.83	0.01	-6.17
44	S Intra degree + E Urban human development	3	20.20	6.10	0.01	-6.30
30	D space use extent + S Intra degree	3	20.20	6.10	0.01	-6.30
15	D sex + S Intra degree	3	20.21	6.10	0.01	-6.30
36	S Intra space use overlap + S Intra degree	3	20.21	6.11	0.01	-6.31
33	D space use extent + E Urban human development	3	20.30	6.20	0.01	-6.35
29	D space use extent + S Intra space use overlap	3	20.31	6.20	0.01	-6.35
13	D sex + D space use extent	3	20.32	6.22	0.01	-6.36
18	D sex + E Urban human development	3	20.33	6.23	0.01	-6.37
39	S Intra space use overlap + E Urban human development	3	20.34	6.24	0.01	-6.37
14	D sex + S Intra space use overlap	3	20.38	6.27	0.01	-6.39

Appendix Table 4. Calicivirus in bobcats on the Western Slope of Colorado, USA.

#	Model	K	AICc	ΔAICc	ω	LL
29	D space use extent + S Intra space use overlap	3	24.02	0.00	0.25	-8.21
38	S Intra space use overlap + S Inter degree	3	25.36	1.34	0.13	-8.88
5	S Intra space use overlap	2	27.07	3.05	0.05	-11.16
4	D space use extent	2	27.31	3.29	0.05	-11.28
7	S Inter space use overlap	2	28.08	4.06	0.03	-11.67
1	Intercept	1	28.10	4.07	0.03	-12.93
37	S Intra space use overlap + S Inter space use overlap	3	28.54	4.52	0.03	-10.47
34	D space use extent + E Urban grid	3	28.57	4.54	0.03	-10.48
40	S Intra space use overlap + E Urban grid	3	29.23	5.21	0.02	-10.82
39	S Intra space use overlap + E Urban human development	3	29.47	5.45	0.02	-10.94
32	D space use extent + S Inter degree	3	29.48	5.45	0.02	-10.94
22	D age + S Intra space use overlap	3	29.55	5.52	0.02	-10.97
42	S Intra degree + S Inter space use overlap	3	29.56	5.54	0.02	-10.98
31	D space use extent + S Inter space use overlap	3	29.59	5.57	0.02	-11.00
30	D space use extent + S Intra degree	3	29.67	5.64	0.01	-11.03
14	D sex + S Intra space use overlap	3	29.68	5.65	0.01	-11.04
9	E Urban human development	2	29.68	5.66	0.01	-12.47
54	E Urban human development + E Urban grid	3	29.80	5.78	0.01	-11.10
41	S Intra space use overlap + E Landscape NDVI	3	29.90	5.87	0.01	-11.15
36	S Intra space use overlap + S Intra degree	3	29.92	5.89	0.01	-11.16
13	D sex + D space use extent	3	30.03	6.00	0.01	-11.21
21	D age + D space use extent	3	30.05	6.03	0.01	-11.23
35	D space use extent + E Landscape NDVI	3	30.06	6.04	0.01	-11.23
10	E Urban grid	2	30.07	6.05	0.01	-12.66
33	D space use extent + E Urban human development	3	30.12	6.10	0.01	-11.26
11	E Landscape NDVI	2	30.45	6.43	0.01	-12.85
49	S Inter space use overlap + E Urban grid	3	30.49	6.47	0.01	-11.45
8	S Inter degree	2	30.56	6.54	0.01	-12.91
3	D age	2	30.57	6.55	0.01	-12.91
2	D sex	2	30.58	6.55	0.01	-12.91
6	S Intra degree	2	30.61	6.59	0.01	-12.93
47	S Inter space use overlap + S Inter degree	3	30.82	6.80	0.01	-11.61
48	S Inter space use overlap + E Urban human development	3	30.83	6.81	0.01	-11.62
24	D age + S Inter space use overlap	3	30.88	6.85	0.01	-11.64
50	S Inter space use overlap + E Landscape NDVI	3	30.93	6.90	0.01	-11.66
16	D sex + S Inter space use overlap	3	30.93	6.91	0.01	-11.66

Appendix Table 5. Toxoplasma in pumas on the WS

#	Model	K	AICc	ΔAICc	ω	LL
1	Intercept	1	8.85	0.00	0.62	-3.14
3	D age	2	11.39	2.54	0.18	-2.69
5	S Intra space use overlap	2	11.40	2.55	0.17	-2.70
22	D age + S Intra space use overlap	3	15.24	6.39	0.03	-2.22

Appendix Table 6. Bartonella in pumas on the WS

#	Model	K	AICc	ΔAICc	ω	LL
1	Intercept	1	12.11	0.00	0.35	-4.77
11	E Landscape NDVI	2	14.43	2.32	0.11	-4.21
8	S Inter degree	2	14.83	2.72	0.09	-4.41
5	S Intra space use overlap	2	14.93	2.82	0.08	-4.46
10	E Urban grid	2	15.23	3.12	0.07	-4.61
7	S Inter space use overlap	2	15.28	3.17	0.07	-4.64
9	E Urban human development	2	15.46	3.36	0.06	-4.73
53	S Inter degree + E Landscape NDVI	3	17.57	5.46	0.02	-3.38
55	E Urban human development + E Landscape NDVI	3	17.76	5.65	0.02	-3.48
41	S Intra space use overlap + E Landscape NDVI	3	18.64	6.53	0.01	-3.92
50	S Inter space use overlap + E Landscape NDVI	3	18.68	6.58	0.01	-3.94
56	E Urban grid + E Landscape NDVI	3	19.18	7.08	0.01	-4.19
52	S Inter degree + E Urban grid	3	19.30	7.20	0.01	-4.25
47	S Inter space use overlap + S Inter degree	3	19.36	7.25	0.01	-4.28
38	S Intra space use overlap + S Inter degree	3	19.42	7.32	0.01	-4.31
54	E Urban human development + E Urban grid	3	19.52	7.42	0.01	-4.36
51	S Inter degree + E Urban human development	3	19.60	7.49	0.01	-4.40
39	S Intra space use overlap + E Urban human development	3	19.60	7.50	0.01	-4.40
37	S Intra space use overlap + S Inter space use overlap	3	19.61	7.50	0.01	-4.40
40	S Intra space use overlap + E Urban grid	3	19.73	7.62	0.01	-4.46
49	S Inter space use overlap + E Urban grid	3	19.96	7.86	0.01	-4.58
48	S Inter space use overlap + E Urban human development	3	20.03	7.92	0.01	-4.61

Appendix Table 7. FIV in pumas on the WS

#	Model	K	AICc	ΔAICc	ω	LL
7	S Inter space use overlap	2	14.43	0.00	0.23	-4.22
1	Intercept	1	14.94	0.50	0.18	-6.18
9	E Urban human development	2	15.65	1.22	0.13	-4.83
37	S Intra space use overlap + S Inter space use overlap	3	16.80	2.36	0.07	-3.00
5	S Intra space use overlap	2	17.33	2.90	0.05	-5.67
2	D sex	2	17.46	3.02	0.05	-5.73
10	E Urban grid	2	18.14	3.70	0.04	-6.07
3	D age	2	18.35	3.91	0.03	-6.17
11	E Landscape NDVI	2	18.35	3.92	0.03	-6.17
24	D age + S Inter space use overlap	3	18.70	4.27	0.03	-3.95
39	S Intra space use overlap + E Urban human development	3	18.73	4.30	0.03	-3.97
50	S Inter space use overlap + E Landscape NDVI	3	18.91	4.48	0.02	-4.06
49	S Inter space use overlap + E Urban grid	3	19.09	4.65	0.02	-4.14
16	D sex + S Inter space use overlap	3	19.18	4.75	0.02	-4.19
26	D age + E Urban human development	3	20.30	5.87	0.01	-4.75
18	D sex + E Urban human development	3	20.44	6.00	0.01	-4.82
14	D sex + S Intra space use overlap	3	21.08	6.65	0.01	-5.14
19	D sex + E Urban grid	3	22.00	7.57	0.01	-5.60
40	S Intra space use overlap + E Urban grid	3	22.01	7.58	0.01	-5.61
22	D age + S Intra space use overlap	3	22.09	7.65	0.01	-5.64

Appendix Table 8. Calicivirus in pumas on the WS

#	Model	K	AICc	ΔAICc	ω	LL
1	Intercept	1	14.03	0.00	0.36	-5.73
5	S Intra space use overlap	2	15.83	1.80	0.14	-4.91
9	E Urban human development	2	16.35	2.32	0.11	-5.17
7	S Inter space use overlap	2	17.37	3.34	0.07	-5.68
11	E Landscape NDVI	2	17.45	3.42	0.06	-5.72
2	D sex	2	17.46	3.43	0.06	-5.73
39	S Intra space use overlap + E Urban human development	3	18.59	4.56	0.04	-3.89
40	S Intra space use overlap + E Urban grid	3	18.59	4.57	0.04	-3.90
37	S Intra space use overlap + S Inter space use overlap	3	20.33	6.30	0.02	-4.76
54	E Urban human development + E Urban grid	3	20.51	6.48	0.01	-4.85
14	D sex + S Intra space use overlap	3	20.62	6.59	0.01	-4.91
41	S Intra space use overlap + E Landscape NDVI	3	20.62	6.59	0.01	-4.91
55	E Urban human development + E Landscape NDVI	3	20.65	6.62	0.01	-4.93
18	D sex + E Urban human development	3	20.84	6.81	0.01	-5.02
48	S Inter space use overlap + E Urban human development	3	21.06	7.03	0.01	-5.13
16	D sex + S Inter space use overlap	3	22.13	8.10	0.01	-5.66
49	S Inter space use overlap + E Urban grid	3	22.14	8.11	0.01	-5.67
50	S Inter space use overlap + E Landscape NDVI	3	22.16	8.13	0.01	-5.68
56	E Urban grid + E Landscape NDVI	3	22.25	8.22	0.01	-5.72
20	D sex + E Landscape NDVI	3	22.25	8.22	0.01	-5.72

Appendix Table 9. Toxoplasma in bobcats on the FR

#	Model	K	AICc	ΔAICc	ω	LL
3	D age	2	22.15	0.00	0.09	-8.62
1	Intercept	1	22.16	0.01	0.09	-9.94
28	D age + E Landscape NDVI	3	23.49	1.34	0.05	-7.75
24	D age + S Inter space use overlap	3	23.62	1.47	0.04	-7.81
10	E Urban grid	2	24.02	1.87	0.04	-9.55
8	S Inter degree	2	24.09	1.94	0.03	-9.58
27	D age + E Urban grid	3	24.15	1.99	0.03	-8.07
5	S Intra space use overlap	2	24.16	2.01	0.03	-9.62
22	D age + S Intra space use overlap	3	24.31	2.16	0.03	-8.16
9	E Urban human development	2	24.45	2.30	0.03	-9.77
11	E Landscape NDVI	2	24.50	2.35	0.03	-9.79
2	D sex	2	24.54	2.39	0.03	-9.81
7	S Inter space use overlap	2	24.56	2.41	0.03	-9.82
6	S Intra degree	2	24.61	2.46	0.03	-9.84
4	D space use extent	2	24.75	2.59	0.02	-9.91
26	D age + E Urban human development	3	25.07	2.91	0.02	-8.53
21	D age + D space use extent	3	25.08	2.93	0.02	-8.54
25	D age + S Inter degree	3	25.17	3.02	0.02	-8.59
12	D sex + D age	3	25.19	3.03	0.02	-8.59
23	D age + S Intra degree	3	25.21	3.05	0.02	-8.60
47	S Inter space use overlap + S Inter degree	3	25.66	3.51	0.02	-8.83
54	E Urban human development + E Urban grid	3	26.03	3.88	0.01	-9.02
19	D sex + E Urban grid	3	26.31	4.16	0.01	-9.16
14	D sex + S Intra space use overlap	3	26.57	4.42	0.01	-9.29
55	E Urban human development + E Landscape NDVI	3	26.63	4.48	0.01	-9.32
38	S Intra space use overlap + S Inter degree	3	26.64	4.48	0.01	-9.32
52	S Inter degree + E Urban grid	3	26.65	4.50	0.01	-9.32
51	S Inter degree + E Urban human development	3	26.68	4.52	0.01	-9.34
36	S Intra space use overlap + S Intra degree	3	26.74	4.59	0.01	-9.37
40	S Intra space use overlap + E Urban grid	3	26.81	4.66	0.01	-9.41
17	D sex + S Inter degree	3	26.81	4.66	0.01	-9.41
42	S Intra degree + S Inter space use overlap	3	26.82	4.67	0.01	-9.41
39	S Intra space use overlap + E Urban human develop	3	26.82	4.67	0.01	-9.41
49	S Inter space use overlap + E Urban grid	3	26.86	4.70	0.01	-9.43
53	S Inter degree + E Landscape NDVI	3	26.96	4.80	0.01	-9.48
44	S Intra degree + E Urban human development	3	26.96	4.81	0.01	-9.48
45	S Intra degree + E Urban grid	3	26.97	4.81	0.01	-9.48
20	D sex + E Landscape NDVI	3	26.97	4.82	0.01	-9.49
29	D space use extent + S Intra space use overlap	3	26.98	4.83	0.01	-9.49
32	D space use extent + S Inter degree	3	26.99	4.83	0.01	-9.49
34	D space use extent + E Urban grid	3	27.06	4.91	0.01	-9.53
41	S Intra space use overlap + E Landscape NDVI	3	27.08	4.92	0.01	-9.54
56	E Urban grid + E Landscape NDVI	3	27.10	4.94	0.01	-9.55
37	S Intra space use overlap + S Inter space use overla	3	27.14	4.98	0.01	-9.57
43	S Intra degree + S Inter degree	3	27.16	5.00	0.01	-9.58
16	D sex + S Inter space use overlap	3	27.30	5.15	0.01	-9.65
48	S Inter space use overlap + E Urban human develop	3	27.37	5.21	0.01	-9.68
18	D sex + E Urban human development	3	27.38	5.23	0.01	-9.69
50	S Inter space use overlap + E Landscape NDVI	3	27.39	5.23	0.01	-9.69
31	D space use extent + S Inter space use overlap	3	27.39	5.24	0.01	-9.70
46	S Intra degree + E Landscape NDVI	3	27.41	5.25	0.01	-9.70
33	D space use extent + E Urban human development	3	27.43	5.28	0.01	-9.72
35	D space use extent + E Landscape NDVI	3	27.47	5.31	0.01	-9.73
15	D sex + S Intra degree	3	27.53	5.38	0.01	-9.76
13	D sex + D space use extent	3	27.62	5.47	0.01	-9.81
30	D space use extent + S Intra degree	3	27.69	5.53	0.01	-9.84

Appendix Table 10. Bartonella in bobcats on the FR

#	Model	K	AICc	ΔAICc	ω	LL
7	S Inter space use overlap	2	9.57	0.00	0.45	-2.32
37	S Intra space use overlap + S Inter space use overlap	3	11.75	2.18	0.15	-1.88
50	S Inter space use overlap + E Landscape NDVI	3	12.58	3.01	0.10	-2.29
1	Intercept	1	14.34	4.77	0.04	-6.03
3	D age	2	15.11	5.54	0.03	-5.09
44	S Intra degree + E Urban human development	3	15.29	5.72	0.03	-3.65
9	E Urban human development	2	15.36	5.80	0.02	-5.22
8	S Inter degree	2	15.72	6.16	0.02	-5.40
5	S Intra space use overlap	2	16.24	6.67	0.02	-5.66
4	D space use extent	2	16.42	6.86	0.01	-5.75
33	D space use extent + E Urban human development	3	16.43	6.87	0.01	-4.22
26	D age + E Urban human development	3	16.45	6.88	0.01	-4.22
6	S Intra degree	2	16.65	7.08	0.01	-5.86
11	E Landscape NDVI	2	16.98	7.41	0.01	-6.03
22	D age + S Intra space use overlap	3	17.62	8.05	0.01	-4.81
38	S Intra space use overlap + S Inter degree	3	17.74	8.17	0.01	-4.87
25	D age + S Inter degree	3	17.79	8.22	0.01	-4.89
21	D age + D space use extent	3	17.92	8.35	0.01	-4.96
28	D age + E Landscape NDVI	3	18.06	8.49	0.01	-5.03
23	D age + S Intra degree	3	18.16	8.59	0.01	-5.08
55	E Urban human development + E Landscape NDVI	3	18.36	8.79	0.01	-5.18

Appendix Table 11. FIV in bobcats on the FR

#	Model	K	AICc	ΔAICc	ω	LL
32	D space use extent + S Inter degree	3	16.02	0.00	0.19	-4.09
30	D space use extent + S Intra degree	3	17.05	1.02	0.11	-4.60
4	D space use extent	2	17.82	1.79	0.08	-6.48
1	Intercept	1	18.11	2.09	0.07	-7.92
56	E Urban grid + E Landscape NDVI	3	18.29	2.27	0.06	-5.22
31	D space use extent + S Inter space use overlap	3	18.94	2.92	0.04	-5.55
33	D space use extent + E Urban human development	3	19.37	3.34	0.04	-5.76
11	E Landscape NDVI	2	19.70	3.67	0.03	-7.42
7	S Inter space use overlap	2	19.86	3.84	0.03	-7.50
35	D space use extent + E Landscape NDVI	3	19.94	3.92	0.03	-6.05
6	S Intra degree	2	19.94	3.92	0.03	-7.54
9	E Urban human development	2	20.26	4.23	0.02	-7.70
10	E Urban grid	2	20.42	4.40	0.02	-7.78
8	S Inter degree	2	20.66	4.64	0.02	-7.90
5	S Intra space use overlap	2	20.69	4.66	0.02	-7.91
21	D age + D space use extent	3	20.74	4.72	0.02	-6.45
34	D space use extent + E Urban grid	3	20.74	4.72	0.02	-6.45
29	D space use extent + S Intra space use overlap	3	20.80	4.77	0.02	-6.48
50	S Inter space use overlap + E Landscape NDVI	3	21.56	5.54	0.01	-6.86
46	S Intra degree + E Landscape NDVI	3	21.91	5.88	0.01	-7.03
48	S Inter space use overlap + E Urban human development	3	22.43	6.41	0.01	-7.29
24	D age + S Inter space use overlap	3	22.55	6.52	0.01	-7.35
23	D age + S Intra degree	3	22.55	6.53	0.01	-7.35
37	S Intra space use overlap + S Inter space use overlap	3	22.57	6.54	0.01	-7.36
55	E Urban human development + E Landscape NDVI	3	22.58	6.56	0.01	-7.37
49	S Inter space use overlap + E Urban grid	3	22.59	6.56	0.01	-7.37
45	S Intra degree + E Urban grid	3	22.61	6.59	0.01	-7.38
41	S Intra space use overlap + E Landscape NDVI	3	22.63	6.61	0.01	-7.39
54	E Urban human development + E Urban grid	3	22.63	6.61	0.01	-7.39
28	D age + E Landscape NDVI	3	22.66	6.63	0.01	-7.41
42	S Intra degree + S Inter space use overlap	3	22.66	6.63	0.01	-7.41
53	S Inter degree + E Landscape NDVI	3	22.68	6.66	0.01	-7.42
36	S Intra space use overlap + S Intra degree	3	22.69	6.66	0.01	-7.42
44	S Intra degree + E Urban human development	3	22.73	6.70	0.01	-7.44
43	S Intra degree + S Inter degree	3	22.81	6.78	0.01	-7.48
47	S Inter space use overlap + S Inter degree	3	22.81	6.79	0.01	-7.48
26	D age + E Urban human development	3	23.23	7.20	0.01	-7.69
51	S Inter degree + E Urban human development	3	23.24	7.22	0.01	-7.70
39	S Intra space use overlap + E Urban human development	3	23.24	7.22	0.01	-7.70
40	S Intra space use overlap + E Urban grid	3	23.25	7.22	0.01	-7.70

Appendix Table 12. Toxoplasma in pumas on the FR

#	Model	K	AICc	ΔAICc	ω	LL
3	D age	2	23.64	0.00	0.15	-9.39
27	D age + E Urban grid	3	24.60	0.96	0.09	-8.37
22	D age + S Intra space use overlap	3	24.62	0.98	0.09	-8.39
1	Intercept	1	25.77	2.14	0.05	-11.75
11	E Landscape NDVI	2	26.27	2.64	0.04	-10.71
56	E Urban grid + E Landscape NDVI	3	26.28	2.64	0.04	-9.22
24	D age + S Inter space use overlap	3	26.43	2.79	0.04	-9.29
28	D age + E Landscape NDVI	3	26.51	2.87	0.04	-9.33
12	D sex + D age	3	26.54	2.90	0.04	-9.35
26	D age + E Urban human development	3	26.62	2.98	0.03	-9.39
23	D age + S Intra degree	3	26.63	2.99	0.03	-9.39
10	E Urban grid	2	26.69	3.05	0.03	-10.92
2	D sex	2	26.92	3.28	0.03	-11.03
9	E Urban human development	2	27.01	3.37	0.03	-11.08
7	S Inter space use overlap	2	27.13	3.49	0.03	-11.14
19	D sex + E Urban grid	3	27.44	3.80	0.02	-9.80
6	S Intra degree	2	27.94	4.30	0.02	-11.54
20	D sex + E Landscape NDVI	3	28.19	4.55	0.02	-10.17
5	S Intra space use overlap	2	28.30	4.66	0.01	-11.72
49	S Inter space use overlap + E Urban grid	3	28.37	4.73	0.01	-10.26
16	D sex + S Inter space use overlap	3	28.83	5.19	0.01	-10.49
41	S Intra space use overlap + E Landscape NDVI	3	28.91	5.27	0.01	-10.53
54	E Urban human development + E Urban grid	3	28.93	5.29	0.01	-10.54
50	S Inter space use overlap + E Landscape NDVI	3	28.93	5.29	0.01	-10.54
55	E Urban human development + E Landscape NDVI	3	28.96	5.32	0.01	-10.56
45	S Intra degree + E Urban grid	3	28.98	5.34	0.01	-10.57
18	D sex + E Urban human development	3	29.26	5.62	0.01	-10.71
46	S Intra degree + E Landscape NDVI	3	29.26	5.62	0.01	-10.71
48	S Inter space use overlap + E Urban human development	3	29.37	5.73	0.01	-10.76
40	S Intra space use overlap + E Urban grid	3	29.64	6.00	0.01	-10.89
14	D sex + S Intra space use overlap	3	29.67	6.03	0.01	-10.91
37	S Intra space use overlap + S Inter space use overlap	3	29.70	6.06	0.01	-10.93
15	D sex + S Intra degree	3	29.74	6.10	0.01	-10.95
39	S Intra space use overlap + E Urban human development	3	29.88	6.24	0.01	-11.02
44	S Intra degree + E Urban human development	3	29.99	6.35	0.01	-11.07
42	S Intra degree + S Inter space use overlap	3	30.02	6.38	0.01	-11.09

Appendix Table 13. Bartonella in pumas on the FR

#	Model	K	AICc	ΔAICc	ω	LL
1	Intercept	1	9.87	0.00	0.19	-3.80
5	S Intra space use overlap	2	10.74	0.86	0.13	-2.94
7	S Inter space use overlap	2	11.34	1.47	0.09	-3.24
6	S Intra degree	2	11.97	2.10	0.07	-3.56
11	E Landscape NDVI	2	12.41	2.54	0.05	-3.78
3	D age	2	12.44	2.57	0.05	-3.79
9	E Urban human development	2	12.46	2.59	0.05	-3.80
22	D age + S Intra space use overlap	3	12.95	3.08	0.04	-2.55
37	S Intra space use overlap + S Inter space use overlap	3	13.09	3.22	0.04	-2.62
41	S Intra space use overlap + E Landscape NDVI	3	13.43	3.56	0.03	-2.79
50	S Inter space use overlap + E Landscape NDVI	3	13.58	3.71	0.03	-2.87
36	S Intra space use overlap + S Intra degree	3	13.64	3.77	0.03	-2.90
39	S Intra space use overlap + E Urban human development	3	13.71	3.84	0.03	-2.93
48	S Inter space use overlap + E Urban human development	3	13.89	4.02	0.03	-3.02
24	D age + S Inter space use overlap	3	14.16	4.29	0.02	-3.16
42	S Intra degree + S Inter space use overlap	3	14.29	4.42	0.02	-3.22
46	S Intra degree + E Landscape NDVI	3	14.48	4.60	0.02	-3.32
44	S Intra degree + E Urban human development	3	14.51	4.63	0.02	-3.33
23	D age + S Intra degree	3	14.94	5.07	0.02	-3.55
28	D age + E Landscape NDVI	3	15.32	5.45	0.01	-3.74
55	E Urban human development + E Landscape NDVI	3	15.39	5.52	0.01	-3.77
26	D age + E Urban human development	3	15.42	5.54	0.01	-3.78

Appendix Table 14. FIV in pumas on the FR

#	Model	K	AICc	ΔAICc	ω	LL
6	S Intra degree	2	19.49	0.00	0.27	-7.32
44	S Intra degree + E Urban human development	3	21.07	1.58	0.12	-6.61
15	D sex + S Intra degree	3	21.57	2.08	0.10	-6.86
23	D age + S Intra degree	3	21.67	2.18	0.09	-6.91
36	S Intra space use overlap + S Intra degree	3	22.23	2.73	0.07	-7.19
42	S Intra degree + S Inter space use overlap	3	22.26	2.77	0.07	-7.21
45	S Intra degree + E Urban grid	3	22.38	2.89	0.06	-7.27
46	S Intra degree + E Landscape NDVI	3	22.40	2.91	0.06	-7.28
11	E Landscape NDVI	2	24.85	5.36	0.02	-10.00
1	Intercept	1	25.30	5.81	0.01	-11.52
2	D sex	2	25.39	5.89	0.01	-10.26
7	S Inter space use overlap	2	25.60	6.11	0.01	-10.37
20	D sex + E Landscape NDVI	3	25.80	6.30	0.01	-8.97
16	D sex + S Inter space use overlap	3	26.28	6.79	0.01	-9.22
9	E Urban human development	2	26.43	6.94	0.01	-10.79
50	S Inter space use overlap + E Landscape NDVI	3	27.13	7.64	0.01	-9.64

Appendix Table 15. Calicivirus in pumas on the FR

#	Model	K	AICc	ΔAICc	ω	LL
11	E Landscape NDVI	2	24.43	0.00	0.11	-9.79
1	Intercept	1	25.30	0.87	0.07	-11.52
2	D sex	2	25.42	0.99	0.07	-10.28
3	D age	2	25.70	1.27	0.06	-10.42
46	S Intra degree + E Landscape NDVI	3	25.75	1.31	0.06	-8.95
20	D sex + E Landscape NDVI	3	25.79	1.36	0.05	-8.97
7	S Inter space use overlap	2	26.13	1.69	0.05	-10.64
50	S Inter space use overlap + E Landscape NDVI	3	26.69	2.26	0.03	-9.42
55	E Urban human development + E Landscape NDVI	3	26.72	2.29	0.03	-9.44
16	D sex + S Inter space use overlap	3	26.75	2.32	0.03	-9.45
28	D age + E Landscape NDVI	3	26.86	2.43	0.03	-9.51
41	S Intra space use overlap + E Landscape NDVI	3	26.87	2.44	0.03	-9.51
10	E Urban grid	2	27.10	2.66	0.03	-11.12
56	E Urban grid + E Landscape NDVI	3	27.35	2.92	0.03	-9.75
12	D sex + D age	3	27.53	3.10	0.02	-9.84
24	D age + S Inter space use overlap	3	27.66	3.23	0.02	-9.91
9	E Urban human development	2	27.75	3.32	0.02	-11.45
19	D sex + E Urban grid	3	27.85	3.42	0.02	-10.00
5	S Intra space use overlap	2	27.89	3.45	0.02	-11.51
6	S Intra degree	2	27.89	3.45	0.02	-11.52
27	D age + E Urban grid	3	27.94	3.51	0.02	-10.05
49	S Inter space use overlap + E Urban grid	3	28.13	3.69	0.02	-10.14
15	D sex + S Intra degree	3	28.23	3.79	0.02	-10.19
22	D age + S Intra space use overlap	3	28.34	3.90	0.02	-10.25
18	D sex + E Urban human development	3	28.36	3.92	0.02	-10.26
14	D sex + S Intra space use overlap	3	28.37	3.94	0.02	-10.26
23	D age + S Intra degree	3	28.48	4.05	0.01	-10.32
26	D age + E Urban human development	3	28.49	4.05	0.01	-10.32
42	S Intra degree + S Inter space use overlap	3	28.85	4.41	0.01	-10.50
37	S Intra space use overlap + S Inter space use overlap	3	28.95	4.52	0.01	-10.55
48	S Inter space use overlap + E Urban human development	3	29.12	4.68	0.01	-10.63
54	E Urban human development + E Urban grid	3	29.68	5.25	0.01	-10.92
40	S Intra space use overlap + E Urban grid	3	30.02	5.59	0.01	-11.09
45	S Intra degree + E Urban grid	3	30.06	5.62	0.01	-11.10